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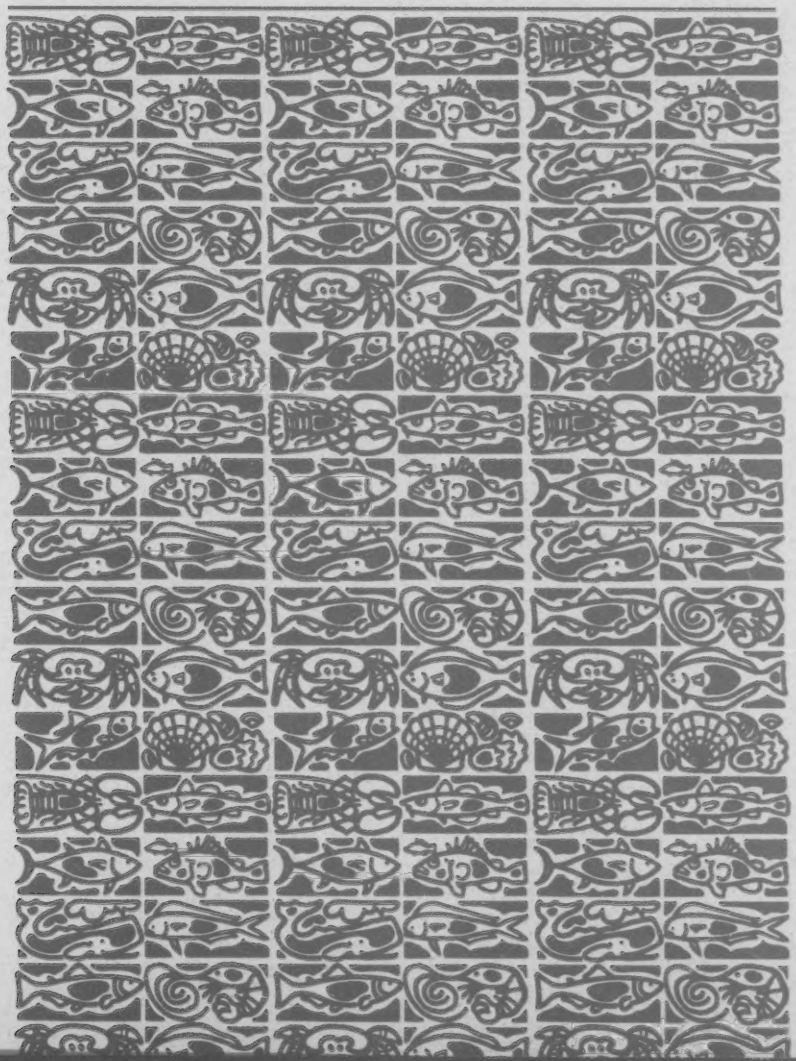

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A probability-based approach to setting annual catch levels

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Abstract—The requirement of setting annual catch limits to prevent overfishing has been added to the Magnuson–Stevens Fishery Conservation and Management Reauthorization Act of 2006 (MSRA). Because this requirement is new, a body of applied scientific practice for deriving annual catch limits and accompanying targets does not yet exist. This article demonstrates an approach to setting levels of catch that is intended to keep the probability of future overfishing at a preset low level. The proposed framework is based on stochastic projection with uncertainty in population dynamics. The framework extends common projection methodology by including uncertainty in the limit reference point and in management implementation, and by making explicit the risk of overfishing that managers consider acceptable. The approach is illustrated with application to gag (*Mycteroperca microlepis*), a grouper that inhabits the waters off the southeastern United States. Although devised to satisfy new legislation of the MSRA, the framework has potential application to any fishery where the management goal is to limit the risk of overfishing by controlling catch.

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The Magnuson–Stevens Fishery Conservation and Management Reauthorization Act of 2006 (MSRA) requires that each Fishery Management Plan in the United States "establish a mechanism for specifying annual catch limits ... at a level such that overfishing does not occur in the fishery ..." (MSRA, 2006). This requirement, which reflects an increased emphasis on conservation, is new in the sense that prevention of overfishing is mandated to be through annual catch limits (ACLs), rather than only through such less restrictive measures as trip limits, size limits, or days allowed at sea. Because the statute requires ACLs to be implemented by 2011 in all fisheries (by 2010 for fisheries where overfishing is occurring), discussion has begun on ways to compute them. Accompanying the discussion of ACLs is the discussion of corresponding annual catch targets (ACTs), levels of catch set as quotas in the fishery.

In this study, we propose a method for setting annual catch levels that are treated as targets, but equally well could serve as limits. The method is based on stochastic projection with uncertainty in population dynamics. It extends usual projection methodology by including uncertainty in the limit reference point and in management implementation, and by making explicit the overfishing risk that managers consider acceptable. This probabilistic approach was devised specifically to satisfy the U.S. statute, but we expect it should be useful whenever the management approach is to limit the risk of overfishing by controlling catch.

From a technical point of view, the requirement to set ACLs is interesting in that overfishing is defined in terms of a fishery input (i.e., fishing-induced mortality rate), yet the control mechanism is defined in terms of a fishery output (i.e., catch). (Review of inputs and outputs in fishery management can be found in Morison [2004] and Walters and Martell [2004].) Values connecting inputs and outputs mathematically are stock abundance and age structure, which change from year to year. Ideally, then, a method to set catch levels would take into account both uncertainty in the estimates of current stock abundance and structure and the expectation that abundance and structure will change with time. Current harvest-control rules for fisheries usually depend on a limit reference point, and uncertainty in estimating the limit reference point should also be considered. The limit reference point (typically the fishing rate at maximum sustainable yield (F_{MSY}) or a proxy for it) is generally considered to represent the level at which overfishing occurs (Mace, 2001).

Given the uncertainties in population dynamics, stock assessment, and fishery management, it is arguably impossible to fish without some risk of overfishing. Rather than attempting to achieve zero probability of overfishing, our approach avoids

overfishing in a probabilistic sense by keeping the expectation of overfishing below a preset level (e.g., 0.1), presumably satisfying the new requirement of the MSRA. The approach is intended for setting annual catch levels while accommodating uncertainties in future stock dynamics, assessment results, and in the implementation of management measures.

Materials and methods

Probability-based approach to setting catch levels (PASCL)

The proposed method acts as a harvest-control rule. It is a probability-based approach to setting catch levels (PASCL), incorporating uncertainties in future stock dynamics, assessment results, and management implementation. Given these uncertainties, PASCL sets annual target levels of catch consistent with the level of risk considered acceptable by managers. The method is based on the ratio-extended approach to setting target reference points (REPAST) of Prager et al. (2003), but is considerably revised 1) to establish reference points in catch, rather than in fishing mortality rate, and 2) to add a stock-projection component, which is needed to set catch for more than one year after a stock assessment. The new method is a general framework that can incorporate details of almost any stock that is assessed. It is illustrated with gag (*Mycteroperca microlepis*), a grouper found off the southeastern United States.

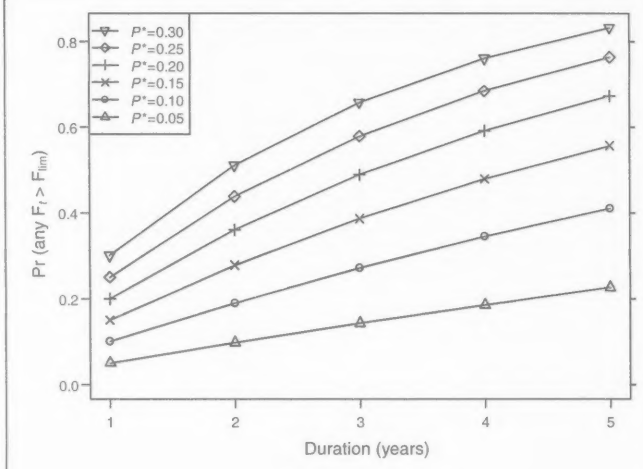

Figure 1

Probability of overfishing in at least one year [Pr(any $F_t > F_{lim}$)] as a function of time duration, assuming independence among years. Probabilities computed for different levels of annual risk P^*.

Uncertainty in stock dynamics is represented by a stochastic projection model. The projection allows the setting of annual catch levels for more than one year and, if necessary, can account for a lag between the final year of assessment data and the first year of management implementation. The projection model need not carry the assumption of equilibrium dynamics and can include any source of process or estimation uncertainty deemed appropriate, as with projections commonly used in fishery management. Sources often considered are recruitment dynamics and initial numbers of fish at age. Modeling nonequilibrium population dynamics, as here, is critical for developing harvest strategies (Hauser et al., 2006).

Stock assessment results generally include estimates of uncertainty. A key stock assessment result used in PASCL is the estimate of F_{lim}, the limit reference point of fishing mortality rate (F) and its associated uncertainty, described by a probability density function (PDF), which can be either parametric or nonparametric. If a PDF of F_{lim} is unavailable, PASCL can use a point estimate, but ignoring that source of uncertainty can make overfishing more likely (Prager et al., 2003). Another basic assessment result, the estimate of stock abundance at age (with the corresponding estimate of uncertainty), is used to initialize stock replicates in stochastic projection with PASCL.

Uncertainty in implementation stems from managers having only partial control of the catch (Rosenberg and Brault, 1993; Caddy and McGarvey, 1996; Prager et al., 2003). A target catch may not be met precisely if catch is monitored with delay, catch is managed indirectly through input controls, regulations are poorly enforced, or fishing behavior is unpredictable.

In PASCL, as in REPAST (Prager et al., 2003), the level of risk acceptable to managers (P^*) is quantified and explicit. In our study, risk is defined as the probability of overfishing in any year t, i.e., as $\Pr(F_t > F_{lim})$. A small value of P^* corresponds to risk-averse management. Always, $P^* < 0.5$ should hold, because at $P^* = 0.5$, overfishing is expected in half of all years. When P^* is defined as a constant probability, the risk of overfishing in at least one of T years grows with the time horizon as $1-(1-P^*)^T$ (Fig. 1).

In a simple formulation, the limit fishing mortality rate F_{lim} could be represented by a point estimate. Then, the probability (here equated to risk) of overfishing in year t would be a function of F_{lim} and the PDF of F_t (ϕ_{F_t}):

$$\Pr(F_t > F_{lim}) = \int_{F_{lim}}^{\infty} \phi_{F_t}(F)dF = 1 - \Psi(F_{lim}), \quad (1)$$

where $\Psi(F_{lim})$ = the cumulative distribution of F_t evaluated at F_{lim}.

A catch level can then be set to position the distribution of F_t so that the desired risk is achieved; i.e.,

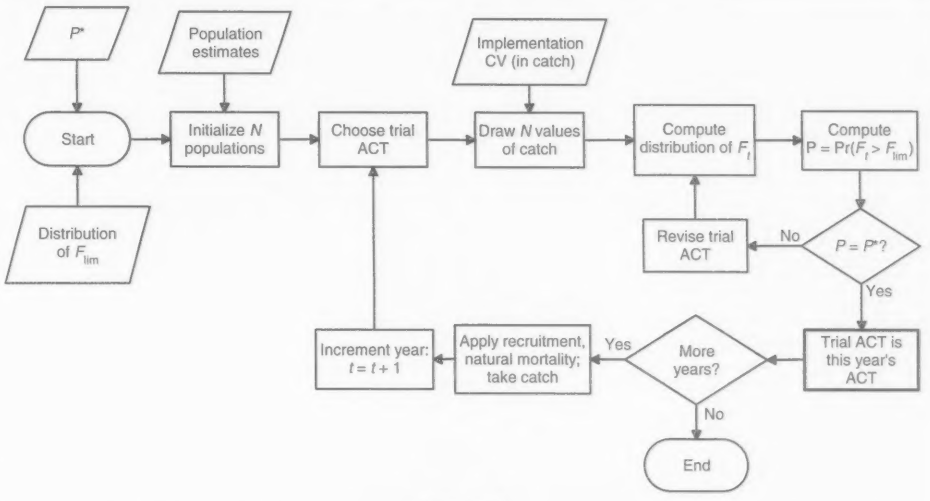

Figure 2

Flowchart of method to compute annual catch level. P^* is the acceptable risk of overfishing, $F_{\lim}$ is the limit reference point in fishing mortality rate, N is the number of replicate projections, ACT is the target annual catch level, CV is the coefficient of variation of management implementation, F_t is the fishing mortality rate in year t of a single projection replicate, and P=Pr(F_t>$F_{\lim}$) is the probability of overfishing in year t associated with a trial ACT.

$\Pr(F_t > F_{\lim}) = P^*$. That catch level becomes the annual catch level in the sense of the MSRA.

The full formulation used here is slightly more complex (and realistic) in that $F_{\lim}$ is described by its PDF, $\phi_{F_{\lim}}$. Then, the probability of overfishing is computed as

$$\Pr(F_t > F_{\lim}) = \int_0^\infty \left[\int_F^\infty \phi_{F_t}(\theta)\, d\theta \right] \phi_{F_{\lim}}(F)\, dF, \qquad (2)$$

where θ = a dummy variable.

Equation 2 is the weighted sum of probabilities computed by Equation 1 for all possible values of $F_{\lim}$. Again, the distribution of F_t can be positioned so that $\Pr(F_t > F_{\lim}) = P^*$.

An assumption of Equation 2 is that $F_{\lim}$ and F_t are independent. If correlation is observed or suspected, the probability of overfishing could be computed from the bivariate PDF $\phi_{F_{\lim},F_t}$,

$$\Pr(F_t > F_{\lim}) = \int_0^\infty \int_F^\infty \phi_{F_{\lim},F_t}\, d\theta\, dF. \qquad (3)$$

Although Equation 3 is more general, estimation of $\phi_{F_{\lim},F_t}$ from data may seldom be possible. Fortunately, in many applications, Equation 2 will be a suitable approximation (see *Discussion* section).

The goal of PASCL is to set annual catch levels such that $\Pr(F_t > F_{\lim}) = P^*$ in each year of a multiyear sequence. Extensions from the formulations described by Equations 1 and 2 are twofold: 1) use of output controls (catches) for management, and 2) a management time frame of more than one year. In what follows, we assume that PASCL is used to compute annual catch targets (ACTs).

The approach is implemented through a projection model (Fig. 2) with the following steps:

1 Initialize N replicates of the stock, each different in abundance and age structure, to reflect uncertainty in the estimated current state of the stock.
2 Given implementation uncertainty in controlling catch, each ACT will be the central tendency of a probability distribution ϕ_C. Choose a trial value of μ, and draw N values $\{C_1 \ldots C_N\}$ from the corresponding distribution. Catch C_1 is the catch taken from stock replicate N_1, C_2 from N_2, and so forth.
3 To combine uncertainties in the state of the stock and implementation, compute for each replicate the fishing mortality rate that yields C_n. This produces N values of F_t to define its empirical probability density (ϕ_{F_t}).
4 Given ϕ_{F_t} and $\phi_{F_{\lim}}$, compute P=Pr(F_t>$F_{\lim}$) from Equation 2.
5 Using a numerical optimization method, adjust μ until P=P^*. The adjusted μ is that year's ACT.

6 Project each replicate one year forward by applying recruitment and natural mortality and taking catch C_n.
7 Repeat steps 2–6 for T years.

In general, duration T of the projection will extend until ACTs based on the next assessment can be implemented. The preceding procedure gives an ACT for each year in the period, and the annual probability of overfishing is kept at P^*.

Setting catch levels of gag

To illustrate the method, we applied PASCL to the gag stock off the southeastern United States. The stock was most recently assessed in 2006 from data through 2004 and a statistical catch-age model (Quinn and Deriso, 1999) including the Beverton–Holt spawner-recruit model (Beverton and Holt, 1957). The stock was estimated to be experiencing the effects of overfishing with a biomass at nearly 90% of that at maximum sustainable yield (SEDAR, 2006). To implement PASCL, we devised a stochastic projection model with structure identical to the age-based assessment model (SEDAR, 2006), in which landings and discards were computed from the Baranov (1918) catch equation. The parameter values chosen were those used or estimated in the assessment.

The projection included two sources of uncertainty in stock dynamics. One was stochasticity in recruitment, assumed to be lognormal about the estimated Beverton-Holt spawner-recruit model, with parameter values from the assessment. The other was uncertainty in the estimated final numbers at age ($\hat{N}_{a,2005}$), which become the initial numbers at age in our example ($N_{a,2005}$). In some applications, the variance of $N_{a,2005}$ would be estimated during the assessment, but SEDAR (2006) provided only point estimates. To include uncertainty, we assumed that multiplicative error in the initial numbers at age followed a lognormal distribution with mean (in log space) of zero and a standard deviation equal to that of recruitment ($\hat{\sigma}_R$):

$$N_{a,2005} = \hat{N}_{a,2005}\exp(\nu), \quad (3)$$

where $\nu \sim N(\mu=0, \sigma=\hat{\sigma}_R)$.

This approach accounts for uncertainty in initial conditions, while maintaining strong year classes estimated in the terminal year of the assessment.

The first year of the projection was 2005, and new regulations on catch levels were implemented in 2008. For the projection during the premanagement years (2005–07), we applied a fixed level of landings, set to the geometric mean of landings from 2002 through 2004. The duration of the projection was 10 years: three premanagement years followed by seven years of managed catch levels (landings plus discard mortalities). Presumably, this duration is generous, spanning a period until the next assessment.

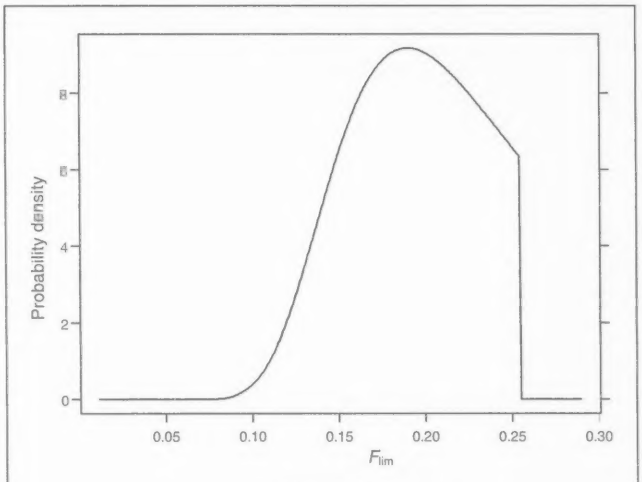

Figure 3

Probability density ($\phi_{F_{lim}}$) of the limit reference point (F_{lim}), defined here as the fishing mortality rate at maximum sustainable yield.

The stochastic projection model was used to generate N=10,000 replicate stocks differing in abundance and age structure. This variation, along with imprecise management implementation, led to N=10,000 values of fishing mortality rate in each year, which were used to characterize the fishery's annual probability density of F_t. These densities (ϕ_{F_t}) were quantified nonparametrically through kernel density estimation with Gaussian kernel and bandwidth equal to the kernel's standard deviation (Venables and Ripley, 2002).

The limit reference point in F was set equal to F_{MSY} (Mace, 2001). For this example, the probability density of F_{MSY} ($\phi_{F_{lim}}$) was estimated after the assessment through Bayesian analysis of the Beverton-Holt spawner-recruit model, accounting for uncertainty in model parameters. A prior distribution was specified for steepness (h), the parameter controlling how quickly recruitment approaches its unfished level as spawning biomass increases. This prior distribution was based on meta-analysis of steepness values (Myers et al., 1999) from species similar to gag. Species included were those considered to be periodic spawners, as defined by Rose et al. (2001), and limited to marine or anadromous demersal fishes, excluding rockfish (*Sebastes* spp.) because of their uncharacteristically low steepness values. The estimated prior distribution was lognormal (SEDAR, 2004):

$$h = \exp(x) : x \sim N(\mu = -0.33, \sigma = 0.28). \quad (4)$$

The resulting posterior distribution of F_{MSY} described $\phi_{F_{lim}}$ for use in PASCL (Fig. 3). In this example, $\phi_{F_{lim}}$

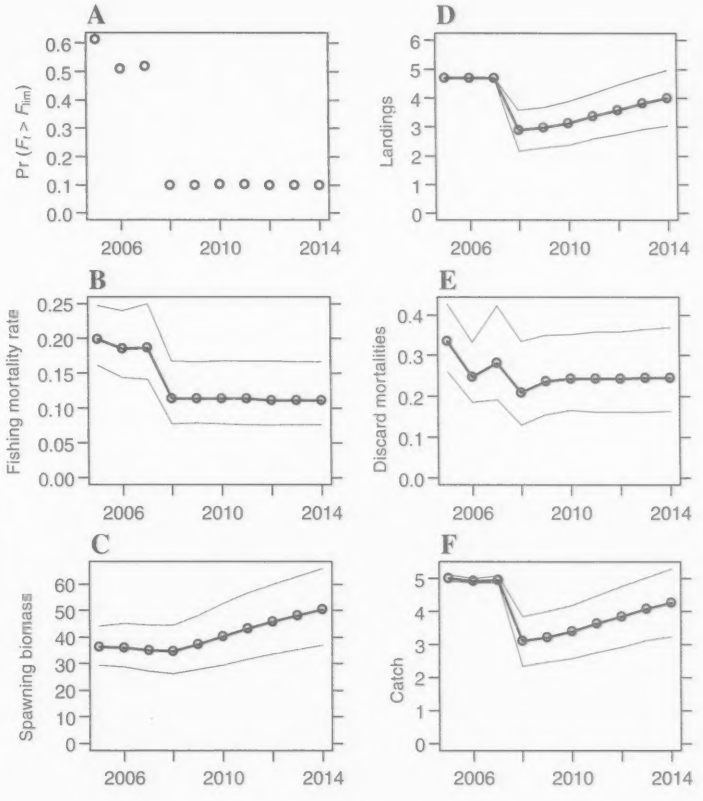

Figure 4

Example projection with managed risk of overfishing set at P^*=0.1 and uncertainty in management implementation described by its coefficient of variation CV=0.2. (**A**) Probability of overfishing, (**B**) annual fishing mortality rate, (**C**) spawning biomass (100 metric tons [t]), (**D**) landings (100 t), (**E**) dead discards (100 t), (**F**) annual catch level (100 t). In B–F, results are presented as medians (thick lines, circles), along with 10th and 90th percentiles (thin lines), from N=10,000 projection replicates.

approaches zero quickly on the right because F_{MSY} is connected tightly with steepness, a bounded parameter with positive probability at its upper bound.

To allow uncertainty in management implementation, the annual catch level was assumed to follow a normal distribution with the mean equal to the target annual catch and coefficient of variation (CV) equal to a preset value. In some applications, the CV of implementation might be estimated from data on performance of the fishery; in this application we considered values of 0.1, 0.2, and 0.3, with a focus on the assumption of CV=0.2.

The final requirement of PASCL is to specify the allowable risk of overfishing. This analysis considered six different levels: $P^* \in [0.05, 0.10, 0.15, 0.20, 0.25, 0.30]$.

Results

During the premanagement period (2005–07), overfishing was projected to occur in at least half of the projections, and thereafter, at the acceptable P^* (Fig. 4A). Because the probability of overfishing in the premanagement period was higher than P^*, the fishing mortality rate was reduced when annual catch targets took effect (Fig. 4B). This allowed spawning biomass to increase (Fig. 4C). With nearly constant F, the increase in biomass provided for an increase in catch, composed mostly of live landings but also dead discards (Fig. 4, D–F). Catch within a year varied by replicate, reflecting uncertainty in management implementation, but by design was centered on the annual catch level (Fig. 4F).

Greater precision in management implementation reduced the variance of F_t for a given catch, which in turn allowed higher fishing mortality rates without an increased probability of overfishing (Fig. 5A). The higher rates then translated into larger annual catch levels (Fig. 5B).

In general, higher P^* was associated with larger catch (Fig. 6A). Biomass increased over time for all P^* examined, but more quickly when risk of overfishing was smaller (Fig. 6B). Consequently, catch increased more quickly for smaller risk, and thus the overall range of catch shrank over time across levels of P^*.

Discussion

The proposed probabilistic approach to setting annual catch levels, PASCL, is quite flexible. It incorporates many of the projection methods common in stock assessment, which can be based on size-structured, age-structured, or unstructured population models. It can incorporate any sources of uncertainty considered important; for example, environmental influences, demographic stochasticity, and multispecies effects. Our work extends common methods by explicitly considering uncertainty in the limit reference point, uncertainty in management implementation, and the level of risk acceptable to managers.

A limit reference point used with PASCL can be a single value, such as F_{MSY} or a proxy for F_{MSY}, but it need not be a single value. For example, the F_{lim} used to manage U.S. west coast groundfish is a function of standing biomass (Punt, 2003). Uncertainty in the limit, whether a single value or function, could be modeled with any appropriate distribution. Similarly, uncertainty in management implementation can be incorporated with flexibility.

Choice of harvest-control rules

PASCL will not be the best choice for setting annual catch levels in every stock. In particular, data-poor stocks will likely require a different approach, such as assemblage management or the use of expert judgment. For rebuilding overfished stocks, other projection approaches may be more suitable (Jacobson and Cadrin, 2002; Punt, 2003). During rebuilding, harvest policies are typically based on the probability of stock recovery within a specified time horizon, rather than on the less restrictive constraint of preventing overfishing. As overfished stocks recover, however, a method such as PASCL could be applied to prevent the stock from another decline and the need for future rebuilding plans.

In one school of thought, choice of a harvest-control rule should be based on the likelihood of meeting long-term management objectives. In this regard, the efficacy of PASCL could be compared to that of other control rules by simulating the assessment and management processes in conjunction with stock dynamics (Cooke, 1999; Punt, 2003). Such management strategy evaluations can be useful for shedding light on which control rules work best under various conditions. However, they are complex, and thus difficult to program, verify, explain, and modify as circumstances change. Moreover, most fishery management is in fact based on short-term to medium-term considerations, and management strategies are likely to change to meet social, biological, or environmental conditions. When a major objective of management is to avoid overfishing, PASCL should be quite effective, and it may simultaneously meet more complex objectives. An advantage of simple control rules such as PASCL is that they can be applied after each assessment without major redesign.

In our example, we computed annual catch levels as targets. With slight modification, the method can be used to compute annual catch limits and targets simultaneously. For example, a catch limit (or acceptable biological catch) might be set to prevent overfishing based on scientific uncertainty (e.g., process and estimation error), and a catch target might then be set lower than the limit to

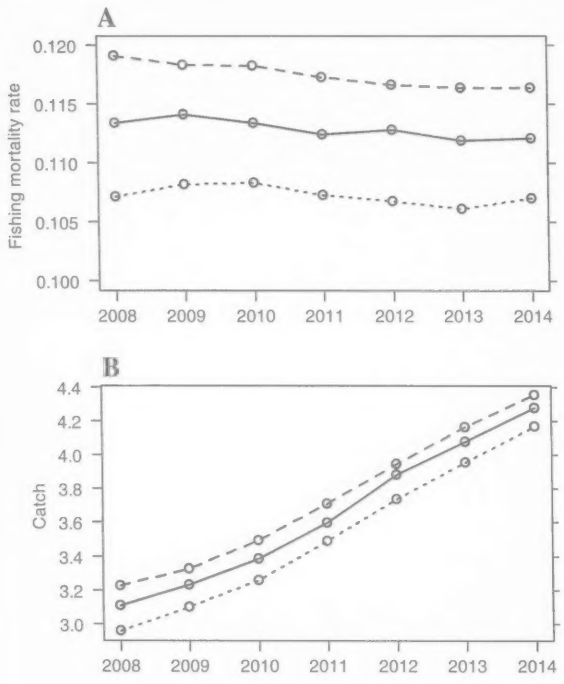

Figure 5

Median annual (**A**) fishing mortality rate and (**B**) catch level (100 t) from projections with managed risk of overfishing set at P^*=0.1 and uncertainty in management implementation, defined by the coefficient of variation CV, set at CV=0.1 (dashed), CV=0.2 (solid), or CV=0.3 (dotted).

account for the implementation of uncertainty. In a projection over multiple years, however, limits and targets should remain coupled, because simulated catch feeds back to abundance levels and thus affects catch levels (limits and targets) in the next year.

Correlation of fishing mortality rates

PASCL, as implemented through Equation 2, implicitly treats the two variables F_{lim} and F_t as independent. In some applications, the two may be correlated. To examine this correlation, we conducted a simulation analysis, in which an age-structured population model was used to generate data that were then used in a catch-age assessment model. In the population model, parameter values representing natural mortality, somatic growth, maturity, fishery selectivity, steepness, recruitment variability, landings, and indices of abundance were generated at random by using levels from other simulation studies (Maunder and Deriso, 2003; Williams and Shertzer, 2003). For simplicity, the simulation included one fishery and one index of abundance. The population was initiated near its unfished state and was subjected to a 27-year linear increase in fishing mortality ranging from 0 to 2 times the rate at F_{MSY} (F_{lim}). Based on 10,000 simulations, the assessment output provided no evidence of correlation between estimates of F_{lim} and terminal-year F_t (r=−0.004, P=0.694), supporting the assumption of independence. In any given application, however, if correlation between F_{lim} and F_t is considered important, PASCL could be applied by using Equation 3.

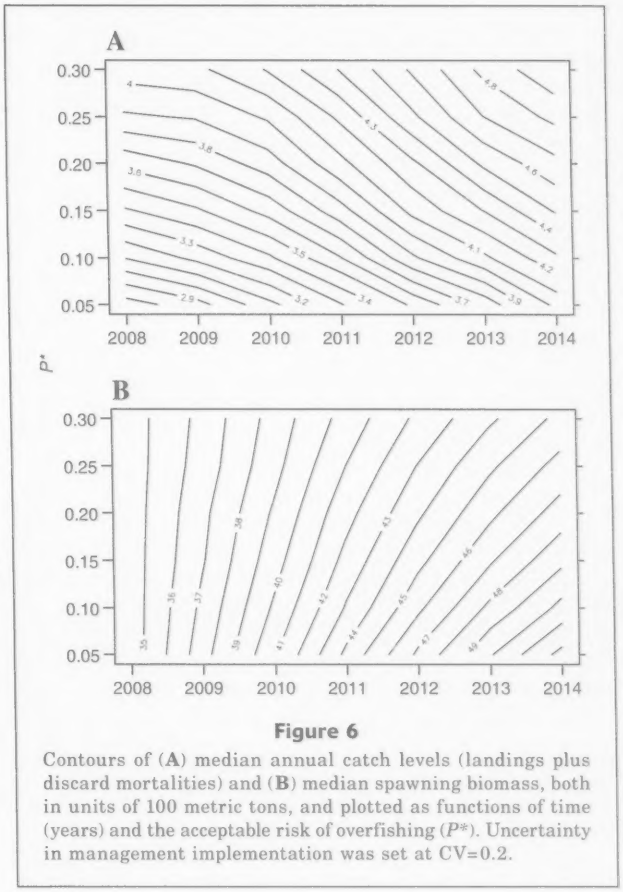

Figure 6

Contours of (**A**) median annual catch levels (landings plus discard mortalities) and (**B**) median spawning biomass, both in units of 100 metric tons, and plotted as functions of time (years) and the acceptable risk of overfishing (P*). Uncertainty in management implementation was set at CV=0.2.

Implementation uncertainty and bias

Uncertainty in implementation is a common, but often ignored, reality of natural resource management (Johnson et al., 1997). This source of uncertainty was quantified here by a normal distribution with an assumed coefficient of variation. In some cases, the distribution could be estimated from data on performance of the fishery—a scenario we expect to become more common as annual catch targets are applied more widely. Our example showed that more precise management allowed higher fishing rates, and thus larger catches, without increased probability of overfishing. Similarly, larger catches would result from more precision in stock dynamics or assessments. This outcome underscores the economic benefits of timely monitoring, enforcement, and compliance.

A notable feature of PASCL is that managers may choose the level of risk that they consider acceptable. This choice could reflect socio-economic considerations, in addition to biological factors such as productivity and vulnerability of the stock. In some cases, higher risk of overfishing may be desired, for example if short term loss of yield outweighs long-term benefits (Shertzer and Prager, 2007). In other cases, managers may be more precautionary. Either way, establishing the level of risk as an explicit choice increases transparency in the management process.

A simplifying assumption of our application was that annual catch, although imprecise, was centered about the target catch level. In many fisheries, however, the distribution of annual catch may be asymmetric in either direction of the target. Such asymmetric distributions can easily be accommodated in PASCL. When annual catch falls above or below the target, managers may consider adjusting target catch in subsequent years accordingly.

Conclusion

Over the next several years, as science responds to legislation, a body of practice will be developed to implement annual catch limits and targets. In managing U.S. federal fisheries, new approaches must address the MSRA requirements to end and prevent overfishing. The

PASCL framework proposed here is intended to satisfy these requirements, and it certainly can be applied more broadly in fisheries where the management of catch levels has the objective of avoiding overfishing.

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A nursery site of the Alaska skate (*Bathyraja parmifera*) in the eastern Bering Sea

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Abstract—A nursery site for the Alaska skate (*Bathyraja parmifera*) was sampled seasonally from June 2004 to July 2005. At the small nursery site (~2 km^2), located in a highly productive area near the shelf-slope interface at the head of Bering Canyon in the eastern Bering Sea, reproductive males and females dominated the catch and neonate and juvenile skates were rare. Seasonal samples showed summertime (June and July) as the peak reproductive time in the nursery although some reproduction occurred throughout the year. Time-series analysis of embryo length frequencies revealed that three cohorts were developing simultaneously and the period of embryonic development was estimated at 3.5 years and average embryo growth rate at 0.2 mm/day. Estimated egg case deposition occurred mainly during summertime and hatching occurred during winter months. Protracted hatching times may be common for oviparous elasmobranch species and may be directly correlated with ambient temperatures as evident from a meta-data analysis. Evidence indicates that the Alaska skate uses the eastern Bering Sea outer continental shelf region for reproduction and the middle and inner shelf regions as habitat for immature and subadults. Skate nurseries may be vulnerable to disturbances because they are located in highly productive areas and because embryos develop slowly.

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Elasmobranchs are of growing concern worldwide because they are threatened by increased fishing and habitat disturbances (Musick et al., 2000; Stevens et al., 2000). Characteristic life history traits of these fish include slow growth rates, late maturation, low fecundity, and long life-spans, all of which make them extremely vulnerable to increased fishing-induced mortality (Dulvy, 1999; Frisk et al., 2002). Species with these life history patterns depend on high juvenile survival and recruitment for population stability. An adequate understanding of reproduction dynamics and habitat requirements are lacking for most species, yet these may be the most critical biological criteria for successful reproduction.

Oviparous species such as skates (Rajidae) use nursery areas for egg deposition, embryo development, and hatching (Hitz, 1964; Hoff, 2007). They produce relatively large collagen egg cases (Knight et al., 1996) which contain a large yolk mass and developing embryo. The egg cases are deposited directly onto the seafloor and embryos develop independent of maternal care (Hamlett and Koob, 1999). The embryonic developmental period is unknown for most species of skates, but evidence indicates that it may exceed one year for temperate and deepwater species (Berestovskii, 1994).

The Alaska skate (*Bathyraja parmifera*) represents >95% of estimated skate biomass on the eastern Bering Sea shelf (20 to 200 m) (Lauth and Acuna, 2007), and estimates of biomass and population numbers have indicated nearly a fourfold increase since 1975 (Hoff, 2006). Skates at all life stages are encountered in the shelf environment and the species range is limited to depths of <400 m on the slope (Hoff and Britt, 2003, 2005; Stevenson et al., 2007). The Alaska skate reaches a large size (135 cm) and can be locally abundant (Hoff and Britt, 2005). Its distribution pattern and accessibility in relatively shallow waters make the species a likely candidate in target fisheries, and its life history characteristics make it susceptible to population decreases (Matta, 2006; Matta and Gunderson, 2007). A nursery site for the Alaska skate was identified in June 2004 (Fig. 1) where significant numbers of skate egg cases were previously reported by commercial fishing crews and fisheries observers. The nursery exists in an area that has been heavily fished for walleye pollock (*Theragra chalcogramma*) and Pacific cod (*Gadus macrocephalus*) for many years, and the site is frequently disturbed by bottom trawls.

Understanding reproductive characteristics and essential habitat requirements are necessary to accurately predict population stability under changing conditions for elasmobranch species worldwide. The recent discovery of a nursery site for the Alaska skate allowed a first look at the reproductive details of the species. Specifically, this study estimates the timing of egg deposition and duration of embryonic development through length-frequency mode tracking from a seasonal sampling of embryos. In addition, the habitat of the Alaska skate is examined with respect to nursery site use and life-stage distribution patterns.

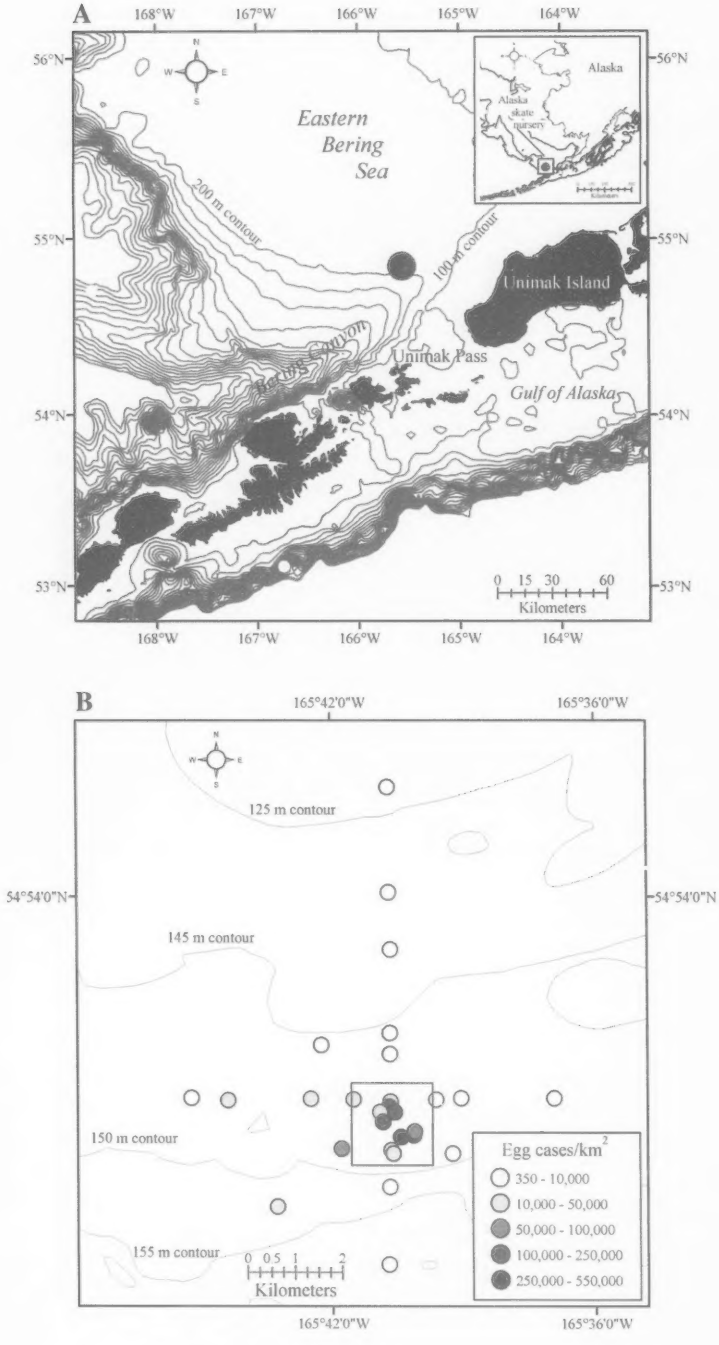

Figure 1

(**A**) Map of the eastern Bering Sea, Alaska, and location of a nursery site (dark circle) for the Alaska skate (*Bathyraja parmifera*) at the head of Bering Canyon. (**B**) Locations at the nursery site for all trawls completed. The area in the box was designated as the index site and targeted for a 14-month seasonal study conducted during 2004–05.

Materials and methods

Sampling at the nursery site

The Alaska skate nursery site was sampled by methods and gear similar to those used by the annual Alaska Fisheries Science Center (AFSC) standard eastern Bering Sea bottom trawl survey (see Lauth and Acuna, 2007). The samples were collected with an 83-112 eastern otter trawl with a 25.3-m headrope and 34.1-m footrope. The footrope consisted of a single firehose-wrapped chain lacking bobbins or discs, and bottom contact was monitored by using electronic tilt sensors designed by personnel at the AFSC. Towing speed varied from 2 to 3 knots and tows were made directly into prevailing currents and wind to help control towing speed. During each tow, starting and ending latitude, longitude, bottom depth, time, vessel speed, net height and width, and bottom temperatures were recorded with NETMIND (vers. 3.0, Northstar Technical Inc., St. John's, Newfoundland, Canada) acoustic trawl mensuration gear. Area swept was estimated from the average net width and distance fished during each tow. Egg case, fish, and invertebrate densities were estimated from the area swept and from the numbers within each category (egg case, fish, and invertebrate) caught in each trawl haul.

An initial exploratory trawl was conducted in June 2004 to locate the skate nursery. A subsequent survey to determine the spatial coverage of the nursery was conducted during July–August 2004. The extent of the nursery area was determined by using an adaptive trawling approach, where 1) trawls were conducted in each of four directions from 0.5 to 1.5 km apart and 2) a reduced egg case density of <500 eggs/km^2 was used as the criterion to indicate the farthest limits of the nursery (Fig. 1). The goal was to map the egg case distribution and estimate the size of the nursery area.

The Alaska skate nursery site was sampled a total of eight times over the 14-month period in June, July, September, and November of 2004 and January, April, June, and July of 2005. An index area was chosen during the July–August 2004 investigation and was sampled during each of the subsequent six seasonal sampling periods (September 2004 to July 2005). The index site was defined as an area where the skate eggs were pre-

dominately in early stages of development (newly deposited) and a large percentage were viable and at high densities (>50,000 eggs/km^2) to allow tracking of embryonic development. The index site constituted an approximate 1-km^2 area where the highest egg case density trawls were located. During each seasonal sampling period, a single 5 to 10 min bottom trawl targeted the index site. The data collected from seasonal samplings were similar to those previously described for the July–August 2004 trawl investigation; however because of time limitations, trawl data were limited to bottom depth, temperature, distance fished, and start and end latitude and longitude during seasonal sampling.

Collection of biological data

All skates were weighed and enumerated, or a weighed numerical subsample was used to estimate total numbers from weighed samples. All egg cases were identified to species and documented as empty (posthatching) or full (prehatching), including eggs that may have been damaged by the trawl. A random sample of full egg cases was fixed in 10% formalin from each sampling period for embryo measurements. Density estimates for skates and egg cases were calculated as the number of eggs encountered per km^2 by using area swept by the net and the number of individuals encountered in each trawl.

All skates encountered were identified to species and sex, and total lengths (TL, to nearest cm) and weights (to nearest 0.1 g) were recorded. Biological data were collected on randomly selected Alaska skates during all seasonal sampling to determine maturity state, reproductive state, and diet composition. During the initial July 2004 sampling, 67 female and 45 male Alaska skates were examined and during all subsequent sampling periods from 2 to 12 males and 5 to 17 females were examined. For each skate sampled the species, sex, total fish length, total fish weight, stomach content weight, and general diet composition were recorded. Reproductive state of males and females were determined by following maturity stages detailed in Matta and Gunderson (2007).

Embryo length-frequency measurements

Formalin-fixed egg cases were neutralized and soaked in tap water for up to four days before measurements were taken. Egg cases were cut open, embryos excised from the yolk, and total lengths (TL) were measured to the nearest 0.5 mm. For analysis, lengths were rounded to the nearest millimeter. Measurements were taken from the anterior tip of the snout or disc to the posterior tip of the tail filament.

Growth rates of Alaska skate embryos were estimated by following methods similar to those used for the juvenile English sole (*Plueronectes vetulus*) off the Washington coast (Shi et al., 1996). Natural mode breaks were used to demarcate cohorts from embryo length frequencies. A mean embryo length was estimated for each cohort at each sampling period and plotted along with the corresponding sampling date. A best-fit linear model was used to determine daily growth rates of each cohort. Embryonic growth was assumed linear throughout development, and the cohort data indicated that the linear model was applicable. Hatching dates were estimated by using a mean hatching size of 224 mm TL (mean of all near hatching embryos, n=39) and the average growth rate from the linear regression. Hatching-date estimates were defined as the time required to reach 224 mm TL based on the length and date of capture. Egg-deposition date was obtained for each embryo measured by back-calculating the time required to reach a size of 1 mm based on the length and date of capture and the average growth rate. An estimate of time between cohorts was calculated as the difference between mean lengths for each cohort divided by daily growth rate to obtain average time between each depositional event.

Analysis of developmental period determined from the literature

A review of previously published studies on hatching duration and rearing temperatures was synthesized for comparison with hatching duration and rearing temperatures obtained from this study. Species in this analysis were limited to oviparous elasmobranchs, which encompassed a diverse group of 13 chondrichthyan fishes: a chimera, the spotted ratfish (*Hydrolagus colliei*), two catshark species (*Scyliorhinus* spp.), and ten species of skates in three genera (*Raja*, *Leucoraja*, and *Okamejei*) (Table 1). Species reviewed were found from subtropical to temperate waters spanning a range of temperatures from 4.6°C to 24°C. Developmental periods and rearing temperatures were obtained from the reported literature for each study. When a range was reported for either developmental period or rearing temperature, an arithmetic mean was calculated from those values. Temperature and embryonic development period were plotted and a nonlinear regression algorithm was applied to the data.

Habitat use

The distribution of life stages of the Alaska skate was investigated by examining bottom trawl survey data from the eastern Bering Sea summertime groundfish survey of the AFSC for years 2000 through 2007 (Lauth and Acuna, 2007). Alaska skate density for each station was estimated as the summed catch per unit of effort (CPUE, number of skates/km^2) obtained at each station for the eight years surveyed. Density estimates were calculated at each trawl station for each life history stage of the Alaska skate: juvenile (≤300 mm TL, newly hatched to age +1); immature (301–920 mm TL); and adults (>920 mm TL, average maturity size; Matta and Gunderson, 2007). Distribution maps were produced with ArcMap (vers. 8.3, Environmental System Research Institute (ESRI) Redlands, CA).

Table 1

Data from reported embryonic developmental periods and developmental temperatures for oviparous elasmobranch species from previously published studies worldwide. Values are the arithmetic means of the reported values.

Common name	Scientific name	Mean developmental period (days)	Mean developmental temperature (°C)	Source
Thorny skate	*Raja radiata*	912	4.6	Berestovskii, 1994
Little skate	*Leucoraja erinacea*	279	10	Steele et al., 2004
Clearnose skate	*Raja eglanteria*	63	24	Libby and Gilbert, 1960
Clearnose skate	*Raja eglanteria*	82	21	Luer and Gilbert, 1985
Clearnose skate	*Raja eglanteria*	85	20	Luer et al., 2007
Clearnose skate	*Raja eglanteria*	368	9.1	Perkins, 1965
Big skate	*Raja binoculata*	277	11.5	Hitz and Reid, 1968*
Spiny rasp skate	*Okamejei kenojei*	137	14.6	Ishihara et al., 2002
Thornback skate	*Raja clavata*	139	14.9	Ellis and Shackley, 1995
Thornback skate	*Raja clavata*	137	15.38	Clark, 1922
Thornback skate	*Raja clavata*	170	14.31	Clark, 1922
Small-eyed ray	*Raja microcellata*	217	14.66	Clark, 1922
Blonde skate	*Raja brachyura*	217	14.13	Clark, 1922
Spotted skate	*Raja montagui*	155	15.93	Clark, 1922
Cuckoo skate	*Leucoraja naevus*	248	13.17	Clark, 1922
Chain catshark	*Scyliorhinus retifer*	256	12.25	Castro et al., 1988
Small spotted catshark	*Scyliorhinus canicula*	165	13.3	Ellis and Shackley, 1995
Small spotted catshark	*Scyliorhinus canicula*	334	10	Thomason et al., 1996
Small spotted catshark	*Scyliorhinus canicula*	205	16	Thomason et al., 1996
Small spotted catshark	*Scyliorhinus canicula*	160	16	Ballard et al., 1993
Spotted ratfish	*Hydrolagus colliei*	300	12.75	Dean, 1906
Alaska skate	*Bathyraja parmifera*	1290	4.4	Hoff (this study)

* Indicates an unpublished study for which the author has the original data.

Results

Sampling of nursery site

The nursery site was relatively small in area, covering approximately 2 km^2 for the highest egg case densities areas. During the initial July–August 2004 nursery investigation, 21 hauls were conducted and egg case densities ranged between 362 and 148,957 eggs/km^2 (mean=19,470 ±36,030 eggs/km^2). A single trawl containing 148,957 eggs/km^2 possessed >70% viable eggs and was designated as an index site for subsequent seasonal trawl sampling (Fig. 1). The seasonal trawl samples contained between 45,418 and 549,843 eggs/km^2 (mean =199,683 ±181,467 eggs/km^2) from the index site and 53–84% of the eggs per tow were viable. The Alaska skate and the Bering skate (*Bathyraja interrupta*) were both found during most sampling periods. The Alaska skate predominated in abundance (96%) and in egg case composition (99.6%). Although the Bering skate accounted for about 4% of the skates found at the site, their egg cases contributed only 0.4%, indicating that this was mainly a single species nursery site for the Alaska skate. The most abundant fish species encountered throughout the sampling period included walleye pollock, arrowtooth flounder (*Atheresthes stomias*), flathead sole (*Hippoglossoides elassodon*), rex sole (*Glyptocephalus zachirus*), and Pacific cod. The most abundant invertebrate species (from summer 2004 trawls) were Tanner crab (*Chionoecetes bairdi*), tentacle-shedding anemone (*Liponema brevicornis*), and Oregon triton (*Fusitriton oregonensis*).

Biological sampling

The size composition of Alaska skate, for all samples combined, indicated that males and females of mature sizes and reproductive state used the nursery nearly exclusively of other posthatching stages; immature and newly hatched juvenile skates were rarely found (Fig. 2). Gonad examination revealed developed ovaries and egg cases in the uterus of female Alaska skates, and fully developed claspers and testes in males during all seasons examined, indicating sexual maturity and that skates were in actively reproducing states. Recent studies have provided evidence that the eastern Bering sea populations of Alaska skate reach a mature state around 93 cm TL for both sexes (Matta and Gunderson, 2007); thus nearly all individuals found within the nursery site of the present study were of reproductive size.

Seasonal nursery use was evident from trawl samples collected at the index site. The Alaska skate showed

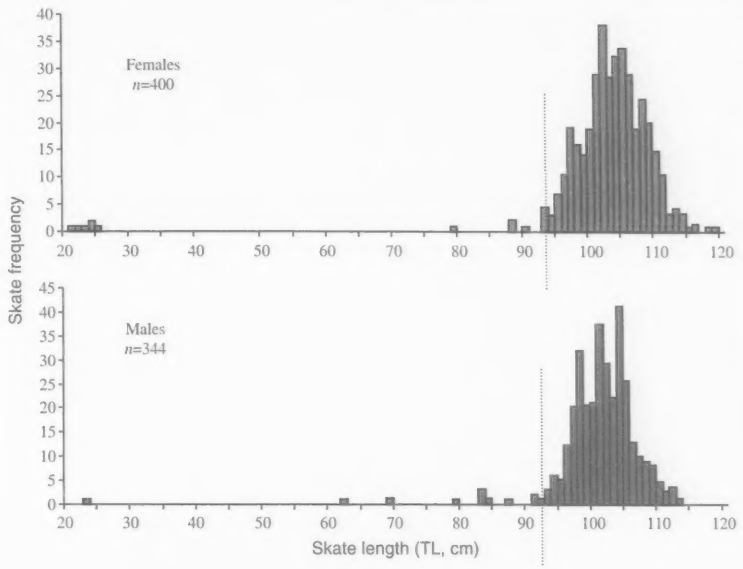

Figure 2

Length frequency for all Alaska skates (*Bathyraja parmifera*) for all trawl samples combined from the nursery site in the southeastern Bering Sea. The vertical dashed line on each graph indicates the skate length at 50% maturity (male, 91.75 cm; female, 93.28 cm) for the eastern Bering Sea Alaska skate population as determined by Matta and Gunderson (2007).

trends of increased abundance (skate density) in the nursery area during summer months of June and July in 2004 and 2005 respectively, and few skates were found during the nonsummer months of January, April, September, and November (Fig. 3).

Stomach analysis of the Alaska skate revealed walleye pollock to be the predominant prey consumed (81% by weight, n=195), followed by other fish species including flatfish, salmon, and unidentified fishes (14.6%), and invertebrate species (snow crabs [*Chionoecetes* spp.] and shrimp that represented the third most important component by weight [4.4%]). Seasonal diet analyses revealed that feeding occurred throughout the year and that skates in advanced reproductive states (gravid) nearly always contained full stomachs.

Embryo length-frequency analysis

Embryo length-frequency modal shifts showed a minimum of three cohorts developing simultaneously during all sampling periods. The mean length of each cohort increased slightly at each subsequent sampling and showed a natural progression of development over time, and individual cohorts appeared and disappeared as time progressed (Fig. 4).

The length data showed that a cohort appeared during the November 2004 sampling and persisted during the April, June, and July 2005 sampling periods. The approximate developmental period was 180 days from egg deposition (June) until the length samples revealed the presence of the cohort (November). The long period of early development was similar to that of the small spotted catshark (*Scyliorhinus canicula*) (Ballard et al., 1993) and the clearnose skate (*Raja eglanteria*) (Luer et al., 2007); for these two species, it takes approximately 15–16% of the early developmental period before an embryo is visible at 8 to 10 mm. This finding was similar to that for the Alaska skate; the smallest embryo visible at 15 mm had taken approximately 14% of the development period to reach this size.

Cohorts 1, 2, and 3 showed no difference in linear growth rates throughout their size ranges (test of slopes F=32.11, P=0.129; Fig. 5). The estimated daily growth rates (slopes) obtained for the cohort length data ranged from 0.18 to 0.22 mm/day (mean: 0.20 mm/day [Table 2]). The distribution of expected birthdates and egg deposition dates from the embryo length frequencies revealed that although there is continuous hatching and egg case deposition throughout the year, the peak hatching event occurs during fall and winter months (October to February: Fig. 6A) and egg case deposition peaks during spring and summer months (June to August: Fig. 6B).

From average growth rates of 0.20 mm/day, an embryonic development period of 3.5 years to reach 224 mm

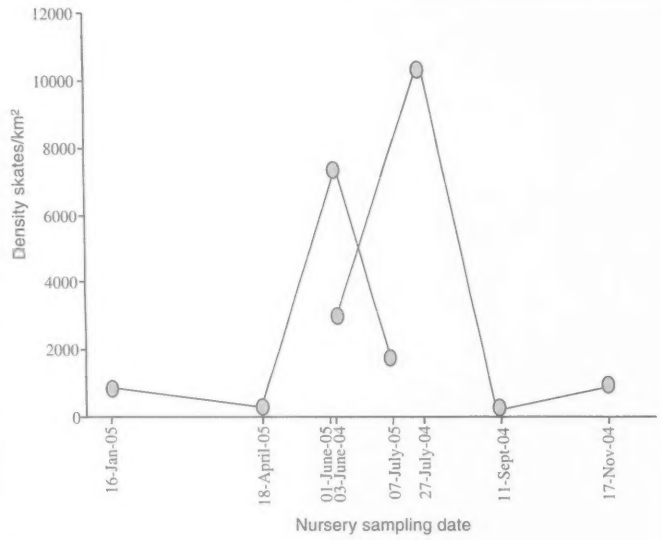

Figure 3

Density estimates of posthatching Alaska skates (*Bathyraja parmifera*) from the eastern Bering Sea nursery site at each seasonal sampling period. Each density estimate was determined from a single tow conducted near the center of the nursery at the index site.

Table 2

Mean length and standard deviation for each cohort of embryos during each sampling period for the Alaska skate (*Bathyraja parmifera*) at the eastern Bering Sea nursery site. A linear regression equation and growth rate for each cohort was estimated from mean embryo lengths. Number of embryos included in each mean length (±1 standard deviation) is denoted by *n*. The time lag between cohorts is the estimated interval between the cohorts—a period determined from mean cohort lengths and growth rates at each sampling period. Cohort 3 had hatched by 18 April 2005 sampling.

Sampling period	Cohort 1 mean length (mm)	*n*	Cohort 2 mean length (mm)	*n*	Cohort 3 mean length (mm)	*n*
3 June 2004	41.6 ±8.09	20	91.5 ±15.12	10	187.89 ±7.88	9
27 July 2004	46.96 ±10.43	23	118.13 ±16.76	8	199.53 ±8.86	15
11 September 2004	57.44 ±8.13	73	131.89 ±12.97	46	207.82 ±9.57	11
17 November 2004	65.24 ±10.33	53	141 ±1.41	2	217 ±12.28	8
16 January 2005	84.17 ±6.19	18	156.38 ±13.31	21	233 ±11.31	2
18 April 2005	97.11 ±7.25	28	171.85 ±18.75	13	Hatching	
1 June 2005	113.83 ±10.25	24	193.27 ±7.92	27		
7 July 2005	116.07 ±11.45	57	200.5 ±0.71	7		
Linear equation	y=0.1819x+13.40		y=0.2214x+68.17		y=0.1899x+ 158.80	
Growth rate of cohort	0.18 mm/day		0.22 mm/day		0.19 mm/day	
Average growth rate			0.20 ±0.02 mm/day			
Time lag between cohort 1 and 2			348.79 ±41.27 days			
Time lag between cohort 2 and 3			411.07 ±44.28 days			

TL was estimated. The time lag between cohorts 1 and 2 was mean=348 ±41 days and between cohorts 2 and 3 mean=411 ±44 days and an overall mean=371 ±50 days between egg deposition events of cohorts one, two, and three combined (Table 2). These data indicate an annual egg deposition cycle, and each cohort represents the result of a single reproductive event that occurs during the summer months.

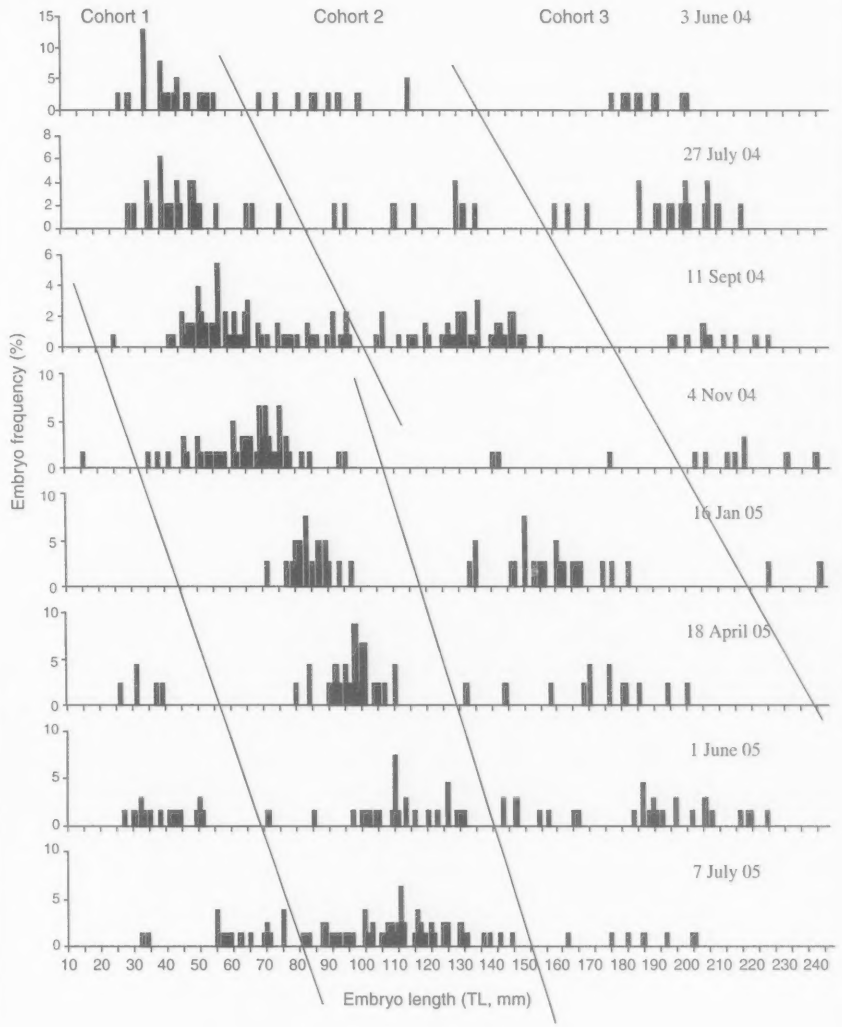

Figure 4

Length frequency for embryos of the Alaska skate (*Bathyraja parmifera*) collected during each sampling date at the nursery index site in the eastern Bering Sea. Embryos were assigned to cohorts 1, 2, or 3 (separated by diagonal lines) following mode frequencies. A fourth cohort was evident that was detected in the November 2004 sampling and persisted through July 2005 (graph left) but was not used for growth-rate estimates.

Analysis of published developmental periods

Developmental period for the Alaska skate was the longest period yet observed for any oviparous elasmobranch species. Embryonic developmental periods were highly correlated with the rearing temperatures for the other oviparous elasmobranchs included in this review (Fig. 7). Most studies were conducted in >8°C water temperatures and developmental periods were one year or less. However, a single study conducted on the thorny skates (*Raja radiata*) (Berestovskii, 1994) in water temperatures near those found for the Alaska skate revealed that the developmental periods of these two species to be comparable (thorny skate, 4.6°C, 912 days; Alaska skate, 4.4°C, 1290 days).

Habitat use

Analysis of trawl catch data and depth soundings showed that the nursery site had little benthic structure or habitat diversity and the bottom was generally flat, and composed of sandy mud. The trawl samples within the nursery did not contain any attached benthic invertebrates that would have constituted a unique habitat. Bottom depths varied by only several meters throughout the nursery site (145 to 150 m) and the average bottom depth was 149 m, weighted by egg case density. Bottom temperatures at the nursery index site varied little throughout the year, ranging between a low of 4.1°C in June 2004 and April 2005, to a high of 5.0°C in July of 2004. The mean bottom temperature for the 14-month study period was 4.40°C ±0.327°C.

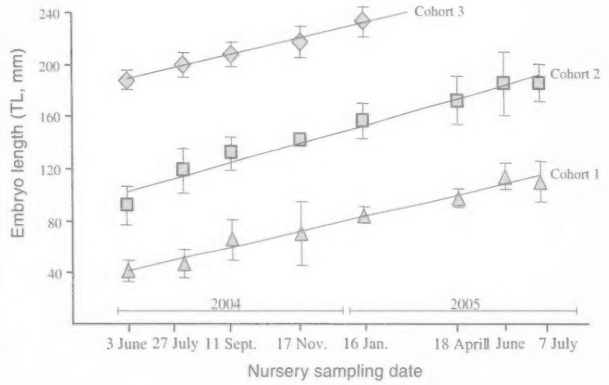

Figure 5

Mean embryo total length (±1 standard deviation) at each sampling date for each cohort from the length-frequency data for the Alaska skate (*Bathyraja parmifera*). Growth rates were estimated from the slope of the linear relationships for each cohort.

The Alaska skate was widely distributed across the eastern Bering Sea shelf and the immature stages used a different portion of the habitat than that used by newly hatched juveniles and mature adults. Juvenile skates were distributed along the outer continental shelf (100–200 m) and overlapped in distribution with mature adults (Fig. 8). Immature Alaska skates were distributed mainly in the middle and inner shelf regions and were found less on the outer shelf. A model lifetime movement pattern for the Alaska skate indicates an ontogenetic shift in habitat use in which there is a cyclical movement across the shelf after hatching to the shallow inner shelf, followed by a return to the outer shelf as maturity is reached (Fig. 8).

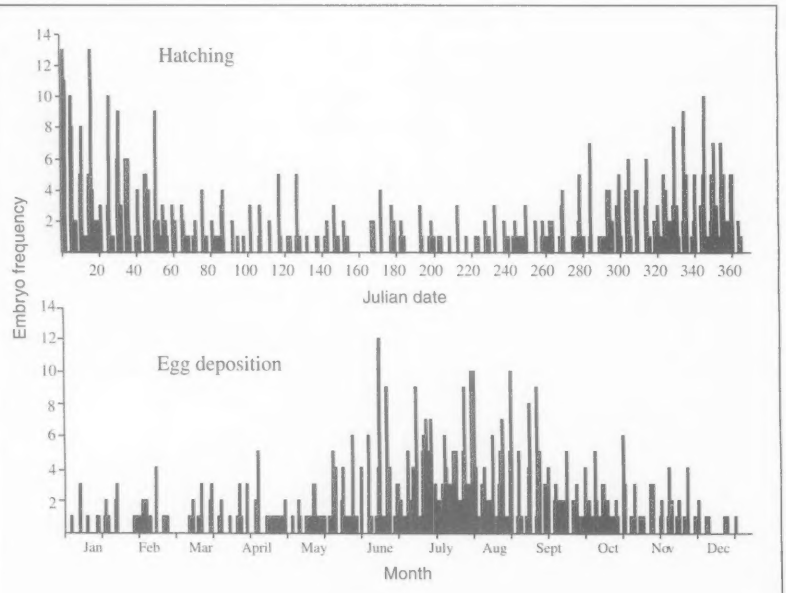

Figure 6

Estimated time of hatching (top) and egg deposition (bottom) frequency for all embryos measured from the Alaska skate (*Bathyraja parmifera*) nursery site. Hatching and egg deposition dates were determined from the average growth rate of 0.2 mm/day and an estimated hatching size of 224 mm total length. The *x*-axis indicates the Julian date (top) and the corresponding month (bottom).

Discussion

Recent advances in elasmobranch biology have stressed the importance of identification and conservation of nursery sites for oviparous elasmobranchs (Ellis et al., 2004). Understanding habitat requirements for skate reproduction may be critical for successful management plans for these vulnerable species. The results presented here are the first reported dynamics of a skate nursery with regard to reproductive patterns and habitat use.

Because of their inherent low fecundity and slow growth rates, skates may reproduce with distinct seasonal pulses, over protracted periods, or in some cases continuously throughout the year (Templeman, 1982; Sulikowski et al., 2005). Results from previous

studies have shown that the Alaska skate is reproductively active year-round and that peak egg production occurs during summer months (Matta, 2006; Matta and Gunderson, 2007). A distinct summertime pulse of egg deposition was evident from the nursery site seasonal skate abundance data, and distinct cohorts of embryos were present in the nursery throughout the year.

Embryonic development of the Alaska skate was estimated to take over 3.5 years from egg deposition until hatching, and as a consequence multiple cohorts were developing simultaneously at the nursery site. Embryonic developmental rates are most likely coupled with environmental temperatures and produce a Q_{10} effect where there is an exponential change in metabolic processes as temperature changes (Schmidt-Nielsen, 1997; Charnov and Gillooly, 2003). The sensitivity of the developmental period to temperature increases is significant; if one uses the regression equation parameters, a mean increase of 0.5°C in environmental temperatures could decrease the developmental period of the Alaska skate by nearly 16% (~6 months) and there would be stronger effects as greater temperature changes occurred. This has dramatic implications on what influence climate change may have on the shelf-slope environment, and skate reproduction and recruitment. The dramatic increase or decrease in recruitment success due to environmental changes may become an important model parameter for stock assessments and management plans for elasmobranch species.

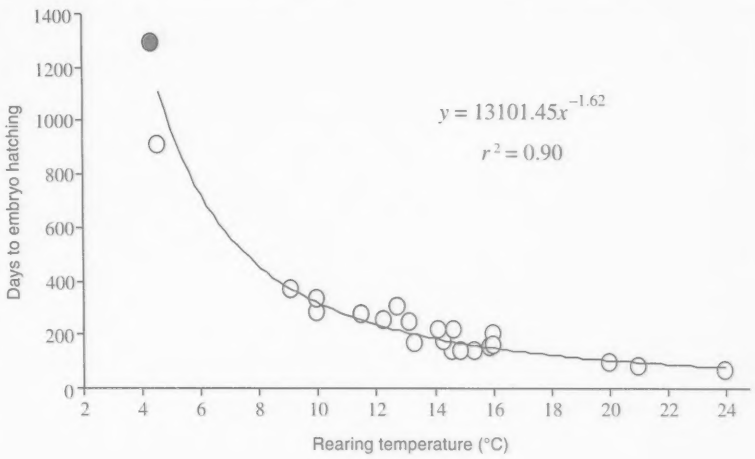

Figure 7

Relationship between rearing temperature and days to hatching determined from 21 published studies and 13 oviparous chondrichthyan species. Open circles represent values from the literature and the shaded circle is estimated embryonic developmental period for the Alaska skate (*Bathyraja parmifera*) in the present study. The hatching time of the Alaska skate was not used to determine the equation parameters. See Table 1 for data sources.

For the estimate of growth rate for the Alaska skate in this study, linear growth was assumed during the developmental period and an effect of environmental temperature on growth rate was not considered because environmental temperatures varied little during this study. These variables recognizably may influence daily growth estimates and therefore the length of developmental period, however averaging across three years of cohorts may provide an accurate estimate of the relatively long developmental period for the Alaska skate, as well as for other oviparous species in cold waters. Linear growth during embryonic development for the size range reported here for the Alaska skate was similar to that for the clearnose skate from approximately 18 mm through hatching (Luer et al., 2007).

Site selection criteria for skate nurseries are as of yet unknown, however areas of high biological productivity may be a requirement for nursery sites because of the protracted reproductive activity and energy requirements of adults. The Alaska skate nursery site is in a region of high slope-shelf water transport and is one of the most productive regions in the eastern Bering Sea (Stabeno et al., 1999); it has supported walleye pollock and Pacific cod bottom trawl fisheries for more than 25 years. Walleye pollock, the main food source of adult Alaska skates (Lang et al., 2005), co-exist in the outer-shelf region during summertime (Kotwicki et al., 2005). Results from the nursery seasonal diet analysis indicated that reproductively active skates feed throughout the year, almost exclusively on walleye pollock. A ready supply of food may allow skates to remain near the nursery site and minimize foraging excursions during protracted reproductive cycles.

Adequate current flows and stable temperatures such as those encountered in the upper slope area of the eastern Bering Sea may be critical for successful hatching and embryo development. From early stages of development, the embryo is dependent on a constant current of fresh seawater to supply tissues with oxygen, remove metabolic waste (Hamlett and Koob, 1999), and prevent the egg case from being buried in sediment. Although strong currents pose a hazard to egg cases by transporting them out of the nursery site, this does not appear to happen frequently because egg cases are rarely found widely scattered outside the nursery, and within nurseries egg cases often cover a small area and are highly concentrated. The upper slope environment provides a nearly constant bottom temperature through upwelled waters that inundate the outer shelf

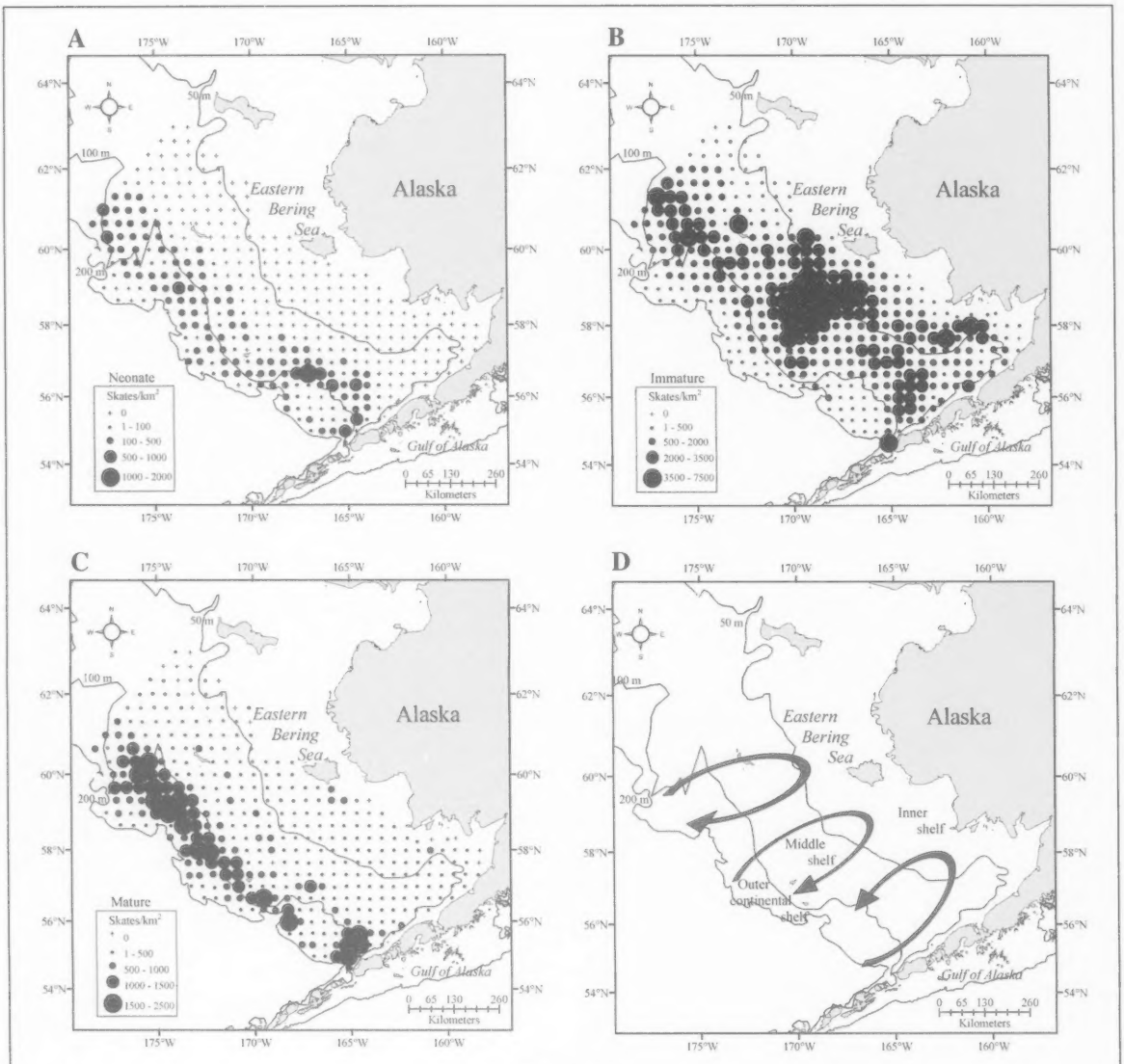

Figure 8

Distribution in the eastern Bering Sea of the Alaska skate (*Bathyraja parmifera*) at three life stages: (**A**) neonate, (**B**) immature, and (**C**) mature. Data are from a summertime (June–July) bottom trawl survey conducted on the eastern Bering Sea shelf from 20–200 m by the Alaska Fisheries Science Center. Dots represent a summation of catch per unit of effort (number skates/km^2) at each survey station for the eight survey years 2000–07. Life stages are defined as the following: neonate < 310 mm total length; immature = 310–920 mm total length; and adult > 920 mm total length. (**D**) Diagram of life-time movement patterns for the Alaska skate in the eastern Bering Sea based on summertime survey data. Young skates are distributed along the outer continental shelf edge where nursery sites occurred. The newly hatched skates move to the middle and inner shelf where they remain until returning to the outer continental shelf at maturity.

(Pavlov and Pavlov, 1996; Luchin et al., 1999) and the nursery experiences relatively stable year-round water temperatures from 4.1° to 5.0°C. By comparison, middle shelf bottom waters are extremely cold throughout the year and may reach <0°C (Luchin et al., 1999; Lauth and Acuna, 2007). Annually the upper slope water may provide the most stable and relatively warm environment for embryo development.

Habitat requirements of newly hatched juvenile skates may not be the criteria for nursery-site selection because very few newly hatched skates were found at the site. The most likely explanation is that neonate skates move out of the nursery area shortly after emergence, possibly to reduce intraspecific competition along the slope edge or to avoid large predators that prey on juvenile skates (Hoff, 2007). In trawl studies with the same designs and methods as those of the present study and conducted across the outer continental shelf region, newly hatched juvenile Alaska skates were found to be common (Kotwicki and Weinberg, 2005; Lauth and Acuna, 2007). Many individuals encountered on the outer shelf still possessed tail filaments, providing evidence of recent emergence from the egg case (Hoff, 2007). The reason why juvenile skate move to inner and outer shelf waters remains unclear; however, a pattern in their movements from inner to outer shelf regions in the eastern Bering Sea and in their use of different habitats at different life stages is evident.

These patterns indicate that skate nurseries may be occupied by skates at two of most critical life stages (embryos and adults), and conservation efforts targeting these stages may have the greatest impact on population protection (Frisk et al., 2002, 2004). Skate nurseries in general may be located in areas of high biological productivity and therefore are susceptible to disturbances caused by increased fishing activities. As oviparous elasmobranch fishing mortality increases, recognition and protection of nursery habitats may be one approach to ensure healthy populations. Likewise, nursery sites may become important locations to be monitored for the health and recruitment potential of skate species. Long-term monitoring of these important habitats can provide a wealth of information with minimal effort because of the permanence or long-term stability of these nursery sites.

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Determination of population structure and stock composition of chum salmon (*Oncorhynchus keta*) in Russia determined with microsatellites

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Abstract—Variation at 14 microsatellite loci was examined in 34 chum salmon (*Oncorhynchus keta*) populations from Russia and evaluated for its use in the determination of population structure and stock composition in simulated mixed-stock fishery samples. The genetic differentiation index (F_{st}) over all populations and loci was 0.017, and individual locus values ranged from 0.003 to 0.054. Regional population structure was observed, and populations from Primorye, Sakhalin Island, and northeast Russia were the most distinct. Microsatellite variation provided evidence of a more fine-scale population structure than those that had previously been demonstrated with other genetic-based markers. Analysis of simulated mixed-stock samples indicated that accurate and precise regional estimates of stock composition were produced when the microsatellites were used to estimate stock compositions. Microsatellites can be used to determine stock composition in geographically separate Russian coastal chum salmon fisheries and provide a greater resolution of stock composition and population structure than that previously provided with other techniques.

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In Asia, there are two distinct types of chum salmon (*Oncorhynchus keta* Walbaum). The early-maturing or "summer" chum salmon generally returns to spawn from June through August in streams bordering Kamchatka, the Sea of Okhotsk, the east coast of Sakhalin Island, and the Amur River. Later-maturing or "autumn" chum salmon generally return to spawn from September through November in streams in Japan, the southern Kuril Islands, the west coast of Sahkalin Island, and the Amur River (Sano, 1966). In general, summer chum salmon spawn in areas where egg incubation occurs in subsurface stream flow, whereas autumn chum salmon spawn in areas of groundwater upwelling (Volobuyev et al., 1990). In major river drainages, autumn chum salmon generally migrate further up the drainage to spawn than do summer chum salmon, and are larger, younger, and more fecund than the summer-run fish (Sano, 1966).

Determination of the origin of salmon in mixed-stock fisheries is important for effective management. For chum salmon in Asia, scale pattern variation has provided a technique for the determination of origin of individuals to large geographic areas (Tanaka et al., 1969; Ishida et al., 1989), and in some cases reportedly to a specific river drainage (Nikolayeva and Semenets, 1983). Trace elements in otoliths have also been reported to be effective for stock identification of Korean populations (Sohn et al., 2005). Stock identification techniques based on scale pattern analysis have generally been replaced by applications based on genetic variation, owing to the increased resolution that is possible by applying genetic variation (see example outlined by Wilmot et al. [1998]). Analyses of genetic variation have been demonstrated to be effective in determining salmonid population structure, as well as determining origins of salmon in mixed-stock fisheries. For Russian chum salmon, analyses of allozyme variation have indicated differentiation among populations on the east and west coasts of Kamchatka (Winans et al., 1994), and either marignal (Salmenkova et al., 2007) or some level of differentiation between populations on Sakhalin Island and populations on the mainland Russian coast (Efremov, 2001). Populations in the far northeastern

portions of mainland Russia were distinct from populations in western Alaska (Wilmot et al., 1994). Surveys of allozyme variation have generally indicated regional population differentiation among Russian populations.

DNA-level markers have substantially increased the number of polymorphic loci that are available to be included in analyses of genetic variation. Initial surveys of mitochondrial (mt) DNA variation indicated regional differentiation between Sakhalin Island and mainland populations (Ginatulina, 1992). Later analyses of additional mtDNA variation indicated marked differentiation between Japanese and Russian populations (Sato et al., 2004), and some differentiation among Russian populations (Brykov et al., 2003; Polyakova et al., 2006). Limited examinations of minisatellite variation have indicated some level of differentiation between Japanese and Russian populations, but have yielded little evidence of regional structure for Russian populations (Taylor et al., 1994; Beacham, 1996).

Analyses of microsatellite variation have been effective for determining salmonid population structure in local areas (Small et al., 1998; Banks et al., 2000; Beacham et al., 2004), as well as broad-scale differences across the Pacific Rim (Beacham et al., 2005, 2006). Microsatellites have also been of considerable value in estimating stock composition in mixed-stock salmon fisheries, on both a population-specific (Beacham et al., 2003) and regional basis (Beacham et al., 2006). Microsatellite variation in chum salmon provides the means to examine fine-scale population structure (Chen et al., 2005), as well as the means for fine-scale estimation of stock composition in mixed-stock fisheries (Beacham et al., in press). Analyses of microsatellite variation in Russian chum populations would likely be of value by providing increased resolution of population structure compared with that provided by previous techniques, and would likely aid in increasing accuracy and precision of estimates of stock composition in mixed-stock fishery samples.

Our objectives were to analyze the variation at 14 microsatellite loci to evaluate population structure of Russian chum salmon populations from the far north eastern coast of Russia to the more southern areas of Primorye and Sakhalin Island, and then to evaluate the use of these loci for the practical purpose of providing accurate and precise estimates of stock composition in mixed-stock fishery samples. Stock composition evaluation was accomplished by the analysis of simulated mixed-stock fishery samples.

Materials and methods

Tissue samples were collected from mature chum salmon at a number of rivers during previous analyses of genetic variation (Winans et al., 1994). Additional tissue samples were sent to the Molecular Genetics Laboratory at the Pacific Biological Station. The geographic area of the 34 populations sampled ranged from Primorye in the south to northeastern Russia (Fig. 1) and encompassed eight geographic regions (Table 1). DNA was extracted from the tissue samples by a variety of methods, including that with chelex resin outlined by Small et al. (1998), a Qiagen 96-well Dneasy® procedure (Qiagen, Mississauga, Ontario, Canada), or a Promega Wizard SV96 Genomic DNA Purification system (Promega, Madison, WI). Once extracted DNA was available, analyses of variation at 14 microsatellite loci were conducted: *Ots3* (Banks et al., 1999), *Oke3* (Buchholz et al., 2001), *Oki2* (Smith et al., 1998), *Oki100* (primer sequence 5′ to 3′ F: GGTGTTTTAATGTTGTTTCCT, R: GTTTCCAGAGTAGTCATCTCTG), *Omm1070* (Rexroad et al., 2001), *Omy 1011* (Spies et al., 2005), *One101, One102, One104, One111,* and *One114* (Olsen et al., 2000), *Ots103* (Nelson and Beacham, 1999), *Ssa419* (Cairney et al., 2000), and *OtsG68* (Williamson et al., 2002).

In general, PCR DNA amplifications were conducted by using DNA Engine Cycler Tetrad2 (BioRad, Hercules, CA) in 6-μL volumes consisting of 0.15 units of Taq polymerase, 1 μL (25–50 ng) of extracted DNA, 1× PCR buffer (Qiagen, Mississauga, Ontario, Canada),

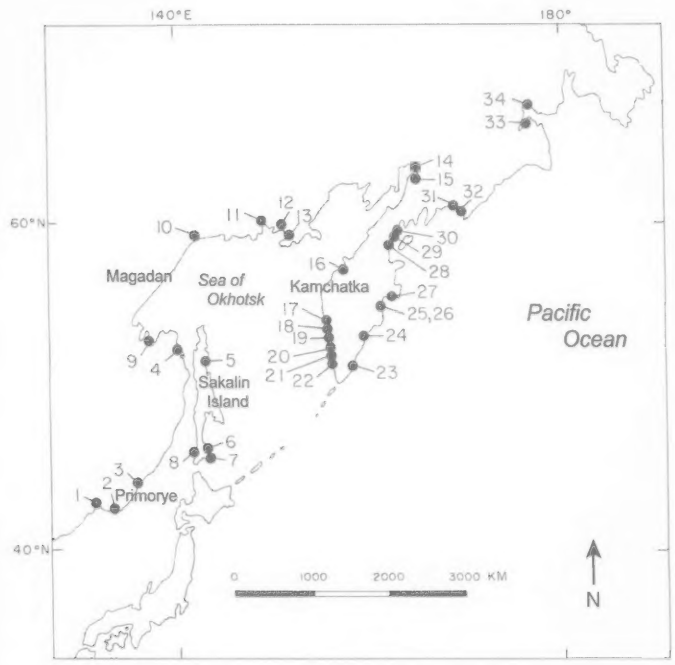

Figure 1

Map indicating the locations in Russia where chum salmon (*Oncorhynchus keta*) from 34 populations or sampling sites were collected. Numbers for and locations of populations are indicated in Table 1.

Table 1

Population, sample collection years, number of fish sampled per year, and total number of fish sampled for 34 populations of chum salmon (*Oncorhynchus keta*) in eight geographic regions from Russia. Eight regions have been defined, and populations (numbered in brackets) were sampled in each region listed. *N* = population size.

Region and population	Years	Annual sample size	*N*
1 Primorye			
Narva [1]	1994	17	17
Ryazanovka [2]	1994	49	49
Avakumovka [3]	1994	35	35
2 Amur River			
Amur River [4]	1994, 2001, 2004	43, 97, 198	338
3 Sakhalin Island			
Tym [5]	1995	55	55
Naiba [6]	1994, 1995	50, 99	149
Udarnitsa [7]	1994	50	50
Kalininka [8]	1994	49	49
4 Magadan			
Tugur [9]	2004	98	98
Okhota [10]	2004	94	94
Magadan [11]	1991	79	79
Tauy [12]	1990	55	55
Ola [13]	1990, 1992	80, 40	120
5 Northern Sea of Okhotsk			
Oklan [14]	1993	76	76
Penzhina [15]	1993	43	43
6 West Kamchatka			
Hairusova [16]	1990, 1993	138, 48	186
Vorovskaya [17]	1991, 1993	79, 170	249
Kol [18]	1991	79	79
Pymta [19]	1992, 1993	40, 59	99
Kikchik [20]	1992, 2005	20, 86	106
Utka [21]	1992	40	40
Bolshaya [22]	2004	96	96
Plotnikova [23]	2001	69	69
7 East Kamchatka			
Zhypanova [24]	2004	46	46
Kamchatka [25]	1990	76	76
Ivashka [26]	2005	48	48
Nerpichi [27]	1992	39	39
Karaga [28]	2005	42	42
Ossora [29]	1990, 1996, 2005	39, 41, 48	128
Dranka [30]	2005	44	44
Apuka [31]	2002	47	47
Olutorsky Bay [32]	2002	49	49
8 Northeast Russia			
Anadyr [33]	1991, 1992	79, 15	94
Kanchalan [34]	1991	79	79

60 μM each nucleotide, 0.40 μM of each primer, and deionized water. The thermal cycling profile involved one cycle of 15 minutes at 95°C, followed by 30–40 cycles of 20 seconds at 94°C, 30–60 seconds at 47–65°C, and 30–60 seconds at 68–72°C (depending on the locus). Specific PCR conditions for a particular locus could vary from this general outline. PCR fragments were initially size fractionated in denaturing polyacrylamide gels by using an ABI 377 automated DNA sequencer, and genotypes were scored by Genotyper 2.5 software (Applied Biosystems, Foster City, CA) using an internal lane sizing standard. Later in the study, microsatellites

were size fractionated in an ABI 3730 capillary DNA sequencer, and genotypes were scored by GeneMapper software 3.0 (Applied Biosystems, Foster City, CA) by using an internal lane-sizing standard. Allele identification between the two sequencers was standardized by analyzing the same approximately 600 individuals on both platforms and converting the sizing in the gel-based data set to match that obtained from the capillary-based set.

Data analysis

Each population at each locus was tested for departure from Hardy-Weinberg equilibrium (HWE) by using genetic data analysis (GDA). Critical significance levels for simultaneous tests (34 populations, Table 1) were evaluated using Bonferroni adjustment (0.05/34=0.0015) (Rice, 1989). All annual samples available for a location were combined to estimate population allele frequencies, as was recommended by Waples (1990). F_{st} estimates for each locus were calculated with FSTAT (Goudet, 1995), individual locus values were determined by jackknifing over populations, and the overall F_{st} estimate was determined by jackknifing over loci (Goudet, 1995). Inter-regional comparisons of F_{st} estimates were determined by calculation of all appropriate pairwise point estimates of F_{st} values, and then determining the mean and standard deviation of these values. The Cavalli-Sforza and Edwards (CSE) (1967) chord distance was used to estimate distances among populations. An unrooted neighbor-joining tree based upon CSE was generated using NJPLOT (Perriere and Gouy, 1996). Bootstrap support (by sampling loci) for the major nodes in the dendrogram was evaluated with the CONSENSE program from PHYLIP (Univ. Washington, Seattle, WA) and based on 500 replicate trees. Computation of the number of alleles observed per locus, as well as allelic diversity standardized to a common sample size, was carried out with FSTAT.

Estimation of stock composition

Genotypic frequencies were determined for each locus in each population, and the Statistical Package for the Analysis of Mixtures software program (SPAM, vers. 3.7, Debevec et al., 2000) was used to estimate stock composition of simulated mixtures. The Rannala and Mountain (1997) correction to baseline allele frequencies was used in the analysis in order to accommodate the occurrence of fish in the mixed sample that were from a specific population having an allele not observed in the baseline samples from that population. All loci were considered to be in Hardy-Weinberg equilibrium, and expected genotypic frequencies were determined from the observed allele frequencies. Reported stock compositions for simulated fishery samples were the bootstrap mean estimate of each mixture of 150 fish analyzed, and mean and variance estimates were derived from 100 bootstrap simulations. Both the baseline population and the simulated single-population were sampled with replacement in order to simulate random variation involved in the collection of the baseline and fishery samples.

Results

Variation within and among populations

The observed number of alleles observed at a locus ranged from 21 alleles at *Oke3* and *Oki2* to 138 alleles at *One111* (Table 2). Lower expected heterozygosities were generally observed at loci with fewer alleles. The genotypic frequencies observed at the 14 loci generally conformed to those expected under Hardy-Weinberg equilibrium (HWE) after Bonferroni correction. For the *Oke3* and *OtsG68* loci, a minor HWE nonconformance of genotypic frequencies was observed, and observed heterozygosities were 2–6% less than those expected (Table 2).

Genetic diversity, with respect to the number of alleles observed, was evident among regional groups of chum salmon. Chum salmon populations from Primorye, the northern Sea of Okhotsk, and northeast Russia displayed fewer alleles (mean 320 alleles) than did populations in Magadan, west Kamchatka, and east Kamchatka (mean 370 alleles) (Table 3). Chum salmon from the latter regions displayed approximately 16% more alleles than did those from the former regions. The greatest differentiation in allelic diversity was observed at those loci with greater numbers of alleles, particularly at locus *One111*.

Population structure

Genetic differentiation was evident among chum salmon populations from the different geographic regions surveyed. The F_{st} value over all 34 populations and 14 loci surveyed was 0.017, and individual locus values ranged from 0.003 (*One102*) to 0.054 (*Ots3*) (Table 2). Chum salmon populations from Primorye and the Amur River were well defined compared with other regional populations (Table 4). Populations from the southwestern portion of Russia (Primorye, Amur River, Sakhalin Island) were most distinct from those in more northern and eastern regions (Magadan, Sea of Okhotsk, Kamchatka, northeast Russia).

Regional clustering of population samples was observed in the analysis of population structure. Strong clustering of population samples from the Primorye region was observed; the three population samples included in the analysis clustered together in 100% of the trees examined (Fig. 2). Similarly, strong clustering was observed in most of the population samples from Sakhalin Island, as well as the two population samples from the northern coast of the Sea of Okhotsk. The two population samples from northeast Russia clustered together in 100% of the trees examined, together with the Utka River population sample from west Kamchatka. Although there was a general clustering of population samples from east and west Kamchatka, these regional

Table 2

Number of alleles per locus, F_{st}, expected heterozygosity (*He*), observed heterozygosity (*Ho*), and percent significant Hardy-Weinberg equilibrium tests (HWE) for 14 microsatellite loci examined in 34 populations of chum salmon (*Oncorhynchus keta*) listed in Table 1. Standard deviation of F_{st} is shown in parentheses.

Locus	Number of alleles	F_{st}	*He*	*Ho*	HWE
Oke3	21	0.050 (0.022)	0.80	0.74	8.6
Oki2	21	0.027 (0.005)	0.87	0.87	2.9
Ots3	26	0.054 (0.014)	0.78	0.78	0.0
Oki100	29	0.015 (0.003)	0.91	0.91	0.0
Ssa419	30	0.010 (0.003)	0.87	0.87	0.0
One102	33	0.003 (0.001)	0.91	0.91	0.0
Omy1011	34	0.010 (0.003)	0.93	0.92	0.0
One104	41	0.013 (0.003)	0.94	0.94	0.0
One101	46	0.052 (0.009)	0.84	0.84	0.0
One114	46	0.015 (0.004)	0.93	0.93	5.7
Omm1070	50	0.005 (0.001)	0.95	0.95	0.0
Ots103	51	0.008 (0.002)	0.95	0.94	0.0
OtsG68	53	0.005 (0.001)	0.95	0.93	8.6
One111	138	0.007 (0.001)	0.98	0.98	0.0
Total		0.017 (0.004)			

Table 3

Mean number of alleles observed per locus at 14 microsatellite loci for 34 chum salmon (*Oncorhynchus keta*) populations from eight regions as outlined in Table 1. Regions were the following: 1) Primorye, 2) Amur River, 3) Sakhalin Island, 4) Magadan, 5) Northern Sea of Okhotsk, 6) West Kamchatka, 7) East Kamchatka, and 8) Northeast Russia. Allele numbers have been standardized to a sample size of 79 fish per region.

	1	2	3	4	5	6	7	8
Oke3	9.0	8.5	9.9	8.7	7.9	8.7	9.7	7.0
Oki100	16.0	18.5	22.3	21.4	17.7	19.6	21.4	19.2
Oki2	14.0	12.1	15.1	14.4	14.7	13.8	16.3	14.5
Omm1070	30.1	26.6	29.0	33.3	27.7	32.3	32.9	29.5
Omy1011	22.0	20.0	22.6	23.7	25.2	22.7	21.8	23.6
One101	20.7	28.3	21.9	25.0	16.6	22.8	23.3	23.1
One102	24.1	19.3	20.1	17.7	16.8	18.5	18.9	14.4
One104	23.8	27.6	23.5	23.9	23.4	24.6	24.9	22.7
One111	51.7	50.8	55.8	71.8	57.9	75.1	71.8	60.7
One114	23.1	24.6	24.0	28.6	19.2	27.3	26.4	25.5
Ots3	12.0	14.1	14.3	14.0	9.7	14.7	16.1	12.9
Ots103	30.0	35.3	38.4	34.4	27.3	35.1	34.4	29.1
OtsG68	32.9	34.2	39.3	35.6	28.7	36.3	36.6	32.7
Ssa419	16.5	14.8	16.0	16.7	14.4	18.7	16.2	11.9
Total	325.9	334.7	352.2	369.2	307.2	370.2	370.7	326.8

groupings were not strongly supported in the cluster analysis.

Stock identification

Genetic differentiation observed among the chum salmon in the regions surveyed was evaluated to determine if it was sufficient for a mixed-stock analysis with the objective of obtaining accurate regional stock compositions. Analysis of simulated single-region samples indicated that estimates of the contribution of chum salmon from that region were usually greater than 89% (Table 5), although there was the expectation that errors in estimation for the region in question would be maximized when the single region comprised 100% of the simulated sample. The level of accuracy observed in the estimated

Table 4

Mean pairwise population F_{st} values observed over 14 microsatellite loci for 34 chum salmon (*Oncorhynchus keta*) populations from eight regions. Regions were the following: 1) Primorye, 2) Amur River, 3) Sakhalin Island, 4) Magadan, 5) Northern Sea of Okhotsk, 6) West Kamchatka, 7) East Kamchatka, and 8) Northeast Russia. Boldface font indicates significant difference ($P<0.05$). A dash indicates that it was not possible to determine within-region pairwise population F_{st} values for the Amur River because only a single population was sampled.

Region	1	2	3	4	5	6	7	8
1	0.012							
2	**0.032**	—						
3	**0.031**	**0.035**	0.020					
4	**0.026**	**0.021**	**0.031**	0.004				
5	**0.036**	**0.036**	**0.046**	**0.010**	0.000			
6	**0.028**	**0.028**	0.027	**0.009**	**0.014**	0.006		
7	**0.026**	**0.024**	0.029	0.006	**0.011**	0.006	0.004	
8	**0.033**	**0.033**	**0.041**	**0.014**	**0.009**	**0.016**	**0.014**	0.000

Table 5

Mean estimated contribution (%) of populations of chum salmon (*Oncorhynchus keta*) in Russia for simulated mixtures. Estimates are for only a single region (correct regional estimate = 100%) and were calculated from the populations listed for each mixture, with each population comprising 50% (100% for Amur River) of each simulated regional mixture. Estimates were determined from 14 microsatellite loci for eight separate regional stocks. The region designation includes percentages allocated to all populations within a region. Simulations were conducted with a 34-population baseline, 150 fish in the mixture sample, and 100 resamplings in the mixture sample and baseline samples. Standard deviations are shown in parentheses.

Mixture	Region	Regional estimate	Population	Population estimate
1	Primorye	89.5 (2.5)	Avakumovka	43.9 (4.5)
			Ryazanovka	45.5 (4.5)
2	Amur River	98.2 (1.1)	Amur	98.2 (1.1)
3	Sakhalin Island	94.8 (1.8)	Naiba	55.1 (4.8)
			Tym	39.6 (4.7)
4	Magadan	90.0 (3.0)	Ola	44.3 (4.5)
			Okhota	44.0 (4.1)
5	Northern Sea of Okhotsk	86.9 (3.1)	Oklan	47.8 (4.7)
			Penzhina	39.1 (4.3)
6	West Kamchatka	95.9 (2.2)	Vorovskaya	49.2 (5.4)
			Hairusova	43.0 (5.2)
7	East Kamchatka	86.1 (3.2)	Ossora	43.9 (4.9)
			Kamchatka	41.2 (4.7)
8	Northeast Russia	89.8 (2.9)	Anadyr	46.5 (4.9)
			Kanchalan	43.3 (3.7)

stock compositions indicated that accurate regional estimates of stock composition should be obtained in samples containing individuals from multiple regions.

Testing of accuracy of regional estimates of stock composition in multiregion mixtures was conducted by evaluating four simulated fishery samples. Estimated stock composition of a simulated mixture containing chum salmon from Primorye, Sakhalin Island, the Amur River, and Magadan was within 3% of the actual population composition and 4% of the regional composition (Table 6, mixture 1). Similar results were observed for a simulated mixture comprising chum salmon from Sakhalin Island, Magadan, the northern Sea of Okhotsk, and west Kamchatka, with population estimates within 3% of actual composition and regional estimates within 3% (Table 6, mixture 2). Estimated stock compositions of a simulated mixture of chum salmon from west Kamchatka, east Kamchatka, and northeast Russia were within 6% of actual population composition and within 5% for regional contributions (Table 6, mixture 3). Regional estimated stock compositions of a more complex simulated sample of fish from

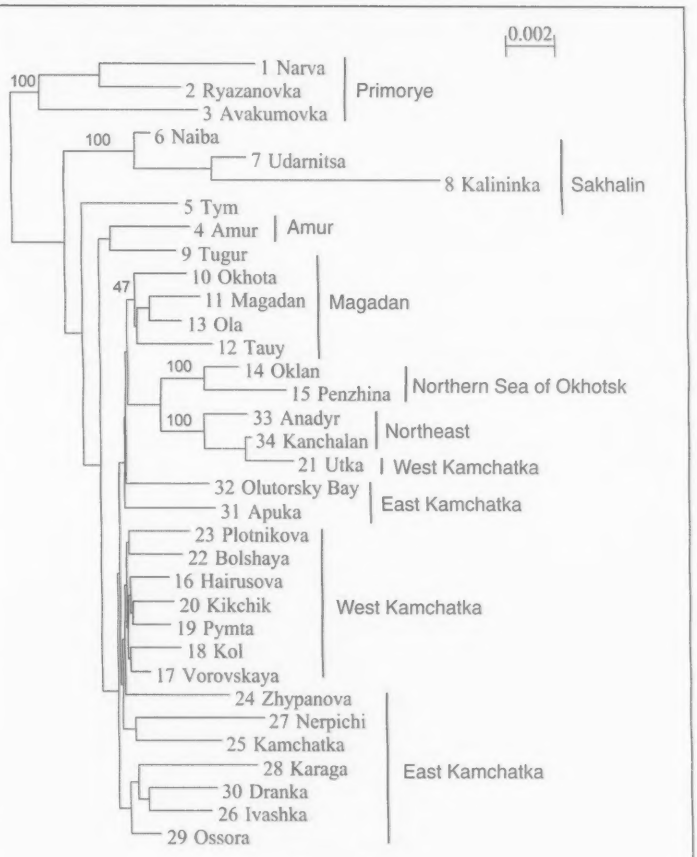

Figure 2

Neighbour-joining dendrogram of the Cavalli-Sforza and Edwards (1967) chord distance for 34 populations of chum salmon (*Oncorhynchus keta*) analyzed at 14 microsatellite loci. Bootstrap values at major tree nodes indicate the percentage of 500 trees where populations beyond the node clustered together. Numbers for and locations of populations are indicated in Table 1.

multiple regions were within 3% of actual regional contributions (Table 6, mixture 4). Accurate regional estimates of stock composition should be obtained when the current baseline is applied to mixed-stock samples of chum salmon taken from Russian coastal waters, provided that the individuals in the mixture originate entirely from Russian populations.

Discussion

Population structure

The range of populations sampled in the study required a concerted sampling effort, and in some locations collection of appropriate samples proved to be difficult. The number of fish sampled from a site or population ranged from 17 to 338 individuals. Estimated population-level allele frequencies will be subject to relatively larger sampling error at smaller population sample sizes, particularly for loci with large numbers of alleles such as *One111*. Small sample size may have contributed to errors on allele-frequency estimates for some populations. Sampling error may obscure genetic relationships among related populations, or conversely genetic relationships among some populations may be falsely inferred. However, the available evidence indicates that variation in population sample sizes did not obscure relationships among related populations. For example, we analyzed chum salmon from three sampling sites in Primorye with sample sizes ranging between 17 and 49 fish per site,. Although these sample sizes were small,

Table 6

Estimated contribution (%) of individual populations and regional estimates of chum chum salmon (*Oncorhynchus keta*) in Russia in simulated mixed-population samples. Each mixture of 150 fish was generated 100 times from baseline allele frequencies, and stock compositions of the mixtures were estimated with parametric resampling of each of the 34 baseline populations to obtain a new distribution of allele frequencies on each iteration. Actual= 100% accurate. Standard deviations are shown in parentheses. Fourteen microsatellites were used to estimate stock compositions of the simulated mixtures.

Populations	Actual %	Estimated %
Mixture 1		
Amur	30	30.5 (4.0)
Avakumovka	10	8.7 (2.0)
Ryazanovka	10	9.1 (2.4)
Naiba	20	21.0 (3.3)
Udarnitsa	10	7.6 (2.2)
Tauy	10	7.1 (2.5)
Ola	10	8.9 (2.5)
Regions		
Amur	30	30.5 (4.0)
Primorye	20	17.9 (3.2)
Sakhalin Island	30	28.7 (3.8)
Magadan	20	16.5 (3.6)
West Kamchatka	0	4.0 (1.9)
East Kamchatka	0	1.6 (1.2)
Mixture 2		
Naiba	20	19.0 (3.2)
Magadan	10	7.8 (2.6)
Ola	10	9.7 (2.8)
Okhota	10	9.0 (2.5)
Oklan	10	7.8 (2.5)
Bolshaya	20	16.5 (3.3)
Hairusova	10	10.0 (3.0)
Kikchik	10	7.5 (2.6)
Regions		
Sakhalin Island	20	19.2 (3.3)
Magadan	30	27.1 (4.0)
Northern Sea of Okhotsk	10	8.0 (2.6)
West Kamchatka	40	42.1 (4.7)
East Kamchatka	0	2.9 (1.6)
Mixture 3		
Plotnikova	20	14.0 (3.3)
Kol	10	6.7 (2.5)
Utka	10	5.5 (1.9)
Kamchatka	10	8.2 (2.4)
Ossora	10	10.6 (2.8)
Olutorsky Bay	10	6.0 (2.6)
Anadyr	20	17.9 (3.4)
Kanchalan	10	12.3 (3.1)
Regions		
West Kamchatka	40	40.8 (4.7)
East Kamchatka	30	25.4 (3.9)
Northeast Russia	30	30.2 (4.1)
Magadan	0	1.4 (1.2)
Northern Sea of Okhotsk	0	1.1 (0.8)
Mixture 4		
Avakumovka	10	8.2 (2.3)
Naiba	10	10.1 (2.3)
Tym	10	8.1 (2.5)
Ola	15	13.0 (2.8)
Okhota	10	8.7 (2.6)
Hairusova	15	13.7 (3.1)
Utka	10	5.5 (2.2)
Kamchatka	10	8.1 (2.5)
Kanchalan	10	11.6 (2.6)
Regions		
Primorye	10	8.3 (2.3)
Sakhalin Island	20	18.3 (3.1)
Magadan	25	22.7 (4.0)
West Kamchatka	25	26.6 (3.8)
East Kamchatka	10	10.9 (2.9)
Northeast Russia	10	12.2 (2.7)

and thus the estimation of allele frequencies would be subject to sampling error, the clustering of these populations was well supported by our bootstrap calculations (100%). Regional clustering of samples or populations is typically observed in chum salmon (Beacham et al., 1987; Winans et al., 1994), and thus it is unlikely that close genetic relationships among these populations from Primorye were inferred incorrectly.

If populations spawn in remote areas, opportunities to collect samples may be limited. In our study, all samples that were available for a specific sampling site or population were combined in order to estimate genetic differentiation among populations. Annual variation in allele frequencies within a population is typically less than the geographic and population differences observed; therefore pooling annual samples over time is a reasonable approach to estimate population-level allele frequencies. Relative annual stability of microsatellite allele frequencies is a general feature of microsatellite loci in salmonids (Tessier and Bernatchez, 1999; Beacham et al., 2006).

The population structure of chum salmon in Russia has been investigated previously. For example, Winans et al. (1994) after examining 35 allozyme loci, indicated that there were four groups of Russian chum salmon populations, and that one group generally comprised populations from west Kamchatka, a second group comprised populations from Magadan, the Sea of Okhotsk, and east Kamchatka, the third group was solely from east Kamchatka, and a fourth group comprised the

populations from the Utka River in west Kamchatka and the Anadyr River in northeast Russia. In our study, some similarities were observed between Magadan and the Sea of Okhotsk regional population groups, as well as between the groups from east and west Kamchatka. Winans et al. (1994) did not include populations from Primorye or Sakhalin Island in their survey, but Ginatulina (1992) had previously demonstrated clear differentiation of mitochondrial genotypes between the populations from these two regions. The results of our study revealed regional separation of populations between these two areas. Our analysis supports the concept of regional groups of populations, and generally supports the concordance in patterns of population differentiation derived from analysis of allozymes and mitochondrial DNA variation. Allendorf and Seeb (2000) reported a concordance between results from allozyme and microsatellite analyses of population structure for sockeye salmon (*O. nerka*).

Genetic differentiation of Russian chum salmon generally follows a regional structure because proximate populations are generally more similar to each other than to more distant populations. However, there were some cases of populations from one region clustering with populations from another region. One example was the Utka River population from west Kamchatka clustering with populations from northeast Russia. An association between the Utka River population and the Anadyr River population was also reported by Winans et al. (1994) in an analysis of allozyme variation. Because Winans et al. (1994) and authors of the present study analyzed the same sample from the Utka River population, concurrence between the allozyme and microsatellite analyses was not unexpected. However, the number of fish sampled for the Utka River population was the fewest for any of the west Kamchatka populations (Table 1), and it may be that an increase in sample size for this population would result in estimated allele frequencies that would be more similar to those of other populations in west Kamchatka. Additionally, the Tugur River population was most closely associated with the population from the Amur River. In recent geologic history, the Tugur River may have been once part of the Amur River drainage, but now flows into Tugur Bay on the Sea of Okhotsk. A common origin between the Amur River and Tugur River populations may account for the current association between the two populations.

Distinctive groups of populations surveyed were those from the Primorye, Sahkalin Island, the northern Sea of Okhotsk, and northeast Russia, and a strong regional clustering of these populations was observed in the dendrogram analysis. Most of these population groups were characterized by slightly lower genetic variation compared with other populations surveyed in Russia. For other salmonids, populations from regions with reduced genetic variation have formed distinctive clusters in dendrogram analysis (Beacham et al., 2006).

Russian chum salmon populations displayed on average less genetic differentiation than did populations from western Alaska and adjacent areas. Despite the Russian populations being surveyed from a larger geographic area than were populations in western Alaska (Beacham et al., in press), and thus there was greater likelihood of differentiation due to isolation by distance, comparisons of locus-specific F_{st} values between the two groups indicated that Russian populations were less differentiated (lower values in 11 of 14 loci, P=0.057). This result indicates that there may be more straying among Russian populations than among those in western Alaska, possibly as a result of adaptation to harsh enviromental conditions or hatchery development and broodstock transfer in Russia. Alternatively, less differentiation would also be observed if Russian chum salmon had colonized available habitats more recently than had chum salmon in western Alaska.

Stock identification

Accurate, economical, and practical methods of stock identification are required to determine the migration pathways of juvenile and maturing salmon, and to manage fisheries that may intercept salmon during their migration to natal spawning grounds. Effective stock identification techniques are based on characters that display stable differentiation among groups to be discriminated, and these characters must be examined easily in a rapid and cost-effective manner. Allozymes provided the characters for initial genetically based population surveys and stock identification of Russian chum salmon (Winans et al., 1994, 1998). Later, single nucleotide polymorphisms (SNPs) were used to estimate the genetic structure of the population (Sato et al., 2001); therefore estimation of stock composition in mixed-stock samples can proceed (Sato et al., 2004). In an analysis of 30 haplotypes from mtDNA, Sato et al. (2004) were able to indicate some level of regional structure in populations in Russia, but the exact nature of the geographic structure was uncertain. In our analysis of microsatellite variation, clear differentiation was observed among regional groups of populations, and populations from Primorye were the most distinctive.

Accuracy of estimated stock compositions is directly influenced by the baseline used in the estimation procedure, and the level of genetic differentiation among regional groups of populations is a key component. However, sample sizes of populations in the baseline are also an important part because the accuracy of estimation is related to the population sample size (Beacham et al., 2006). Fewer than 60 fish were sampled for many of the populations sampled in our survey, and increasing sample sizes to approximately 150 fish per population would likely lead to all regional estimates of stock composition being in excess of 90% accurate in all simulated single-region mixture samples.

Surveys of genetic variation of salmon populations allow stock identification in mixed-stock fisheries, where the origins of fish contributing to mixed-stock fisheries are determined by comparing the genetic characteristics of fish in the fishery samples to the genetic characteristics of fish from potentially contributing populations.

Analysis of simulated mixed-stock samples of known origin is an initial practical method to evaluate the potential for applying genetic variation to mixed-stock fishery analysis. Our analysis of simulated mixtures indicated that microsatellite variation provides accurate estimates of regional contributions of chum salmon stocks from Russia, and in some cases provides reliable estimates of individual populations in simulated mixtures. Microsatellites have previously been reported to provide reliable estimates of stock composition in mixed-stock chum salmon samples of largely North American origin (Beacham et al., in press), and our results from simulated mixtures indicated that microsatellites should provide reliable estimates of stock composition for chum salmon in coastal waters in Russia. However, if Japanese or Korean chum salmon or potentially North American chum salmon are intercepted in coastal or nearshore fisheries in Russia, then clearly a larger baseline than the one examined in the current study would be required to provide reliable estimates of stock composition under these circumstances.

The application of microsatellites for the determination of population structure of Russian chum salmon will allow significant regional differentiation among these populations to be employed in estimating regional contributions to mixed-stock fishery samples from coastal waters. Microsatellites provide similar results for other Pacific salmon species (Beacham et al., 2005, 2006) and are likely to be effective in identifying the origin of Russian chum salmon in mixed-stock fisheries in nearshore and offshore waters.

The present analysis of microsatellite variation of Russian chum salmon provides evidence of a more fine-scale population structure than those that have previously been demonstrated with other genetic-based markers such as allozymes (Winans et al., 1994; Efremov, 2001) or mitochondrial based SNPs (Sato et al., 2004). This more fine-scale resolution of population structure was likely due to the larger number of alleles associated with the microsatellite loci than with either the allozyme or SNP loci. Because genetic-based markers generally exhibit annual stability in allele frequencies, they are generally more effective for stock identification applications than are techniques that rely on environmentally induced variation to discriminate among stocks, such as scale-pattern analysis of trace elements in otoliths. Once the baseline has been established for genetic applications, annual surveys of contributing stocks are not necessary, as is the case with for environmentally induced variation. Should greater resolution in stock composition estimates be required than that provided by the 14 microsatellites surveyed in the present study, the addition of markers specifically designed to provide the required resolution will be necessary. These markers could either be additional microsatellites, or perhaps single nucleotide polymorphisms (SNPs) (Smith et al., 2005). It is likely that a combination of microsatellites and SNPs can be employed to provide accurate population or regional estimates of stock composition of mixed-stock samples.

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Fish assemblages and indicator species: reef fishes off the southeastern United States

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Abstract—For many fish stocks, resource management cannot be based on stock assessment because data are insufficient—a situation that requires alternative approaches to management. One possible approach is to manage data-limited stocks as part of an assemblage and to determine the status of the entire unit by a data-rich indicator species. The utility of this approach was evaluated in analyses of 15 years of commercial and 34 years of recreational logbook data from reef fisheries off the southeastern United States coast. Multivariate statistical analyses successfully revealed three primary assemblages. Within assemblages, however, there was little evidence of synchrony in population dynamics of member species, and thus, no support for the use of indicator species. Nonetheless, assemblages could prove useful as management units. Their identification offers opportunities for implementing management to address such ecological considerations as bycatch and species interrelations.

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Most approaches to fishery management rely on results from stock assessment. Data-limited situations, however, may not conform to conventional assessment methods, necessitating other approaches to management (Kruse et al., 2005). One possible approach with data-limited stocks is to assign them to assemblages that are managed as units. Ideally, each assemblage would include at least one data-rich species that could be assessed and serve as a status indicator of the entire unit. Managing assemblages by means of indicator species is arguably a small but practical step in the direction of ecosystem-based management (Hall and Mainprize, 2004).

Assemblages may be defined by similarities in such biological characteristics as life history, trophic behavior, or home range. For the purpose of fishery management, however, an assemblage should consist of species caught together, if regulations on fishing are to benefit assemblage members. This is particularly true if regulations are focused on an indicator species but the intent is also to control the harvest of other species in the assemblage.

Indicator species have been used in management of both terrestrial and marine systems (Simberloff, 1998; Zacharias and Roff, 2001). The term "indicator species" has no single definition (Landres et al., 1988); it is used here as suggested by the National Standard Guidelines of U.S. federal fishery management, which states that where maximum sustainable yield (MSY) cannot be specified for each stock of a mixed-stock fishery, then "MSY may be specified on the basis of one or more species as an indicator for the mixed stock as a whole or for the fishery as a whole." (Federal Register, 1998) According to this usage, the stock status of the indicator is extrapolated to represent that of other species in the assemblage, or analogously, other stocks of the same species. Such an approach requires the assumption that population trends of an indicator species reflect those of others in the assemblage.

The approach of managing multispecies assemblages by means of indicator species raises two fundamental questions. First, can assemblages be identified? As mentioned, species of an assemblage would need to be caught together if regulations are to affect the entire unit. Second, if an assemblage can be identified, do its members have similar stock dynamics? If not, focusing management on the indicator species may not provide the intended benefits to other stocks.

We address both questions, using as a case study the snapper-grouper complex off the southeastern United States. As defined for management, the complex contains 73 species (Appendix), the majority of which cannot be assessed with currently available data. The objectives of this study are 1) to identify assemblages of finfish species within the snapper-grouper complex and 2) to examine synchrony of stock dynamics within assemblages. To accomplish the first objective, multivariate statistical techniques

were applied to data from recreational and commercial fisheries, and to accomplish the second, indices of abundance were computed and tested for correlation.

Materials and methods

Data used in multivariate analyses

To identify assemblages of species within fishery landings, statistical grouping techniques were applied to two fishery data sets, one recreational (headboat) and one commercial. Both data sets encompassed areas from Cape Hatteras, North Carolina to Key West, Florida. These data were chosen because of their importance for stock assessment of species in the snapper-grouper complex.

The recreational sector was represented by logbook data reported by headboat operators and verified by port samplers. Headboats are large, for-hire vessels that typically accommodate 20–60 anglers on half- or full-day trips. Data collection began in 1972 with a focus on coastal waters off North and South Carolina. The area of collection was extended in 1976 to include the coastal waters of Georgia and northern Florida, and again in 1978 to include those of southern Florida. We used 1972–2005 headboat data. Records from each trip contained information on number of anglers, trip duration, date, geographic area, and landings (number fish) of each species.

The commercial sector was represented by logbook data reported by commercial anglers with snapper-grouper permits. We used 1992–2006 commercial data; however, 2006 was a partial year (data through September). Records contained information similar to those in the headboat data set, but landings were reported in weight (pounds). Excluded were nonsensical records suspected to be misreported or misrecorded. Analyses of commercial data were restricted to trips with handline gear (~87% of records) to avoid the possibility of confounding estimated assemblages with effects of gear. Furthermore, these analyses included only trips of one-day duration (~50% of records) to minimize the possibility that catch in a trip was taken from widely separated geographic areas with potentially different assemblages.

Species assemblages

Following Lee and Sampson (2000), we used more than one statistical technique to identify species assemblages. We applied three techniques: ordination and two types of cluster analysis. For all three techniques, the Sørenson (also called Bray-Curtis) measure of dissimilarity (distance) between species was used (McCune and Grace, 2002). In comparison to other measures, Sørenson distance has been found more robust in ecological studies (Field et al., 1982; Faith et al., 1987) and provides more ecologically interpretable results (Beals, 1973). Perhaps for these reasons, it has been considered appropriate in studies of fish assemblages (e.g., Mueter and Norcross, 2000; Gomes et al., 2001; Williams and Ralston, 2002).

To compute dissimilarities, we formatted each data set as a matrix, with rows representing species and columns representing vessel-months. That is, each element (c_{ij}) of the matrix quantified the amount (in units of number fish for headboat or pounds for commercial) of a species (i) landed by each vessel pooled over one month (vessel-month j). The duration of a month was chosen as a reasonable compromise between maximizing the variety of species landed (longer duration) and minimizing the number of different locations fished (shorter duration). Locations fished per vessel were generally consistent within a month, but could have changed on the time scale of seasons (perhaps following fish migrations, for example). Species were removed if they appeared in fewer than 1% of all trips because rare species may distort inferred patterns (Koch, 1987; Mueter and Norcross, 2000). This restriction left 25,293 records of vessel-month-species in the headboat data set and 143,426 in the commercial data set.

Before computing dissimilarities, data were transformed with the root-root transformation to moderate the influence of abundant species:

$$c'_{ij} = \sqrt{\sqrt{c_{ij}}} = \sqrt[4]{c_{ij}} \quad (1)$$

This transformation has been preferred for density and biomass data, particularly when used in connection with the Sørenson measure of distance (Field et al., 1982). After transformation, a matrix of dissimilarities between species was computed with the Sørenson measure of distance:

$$D_{ih} = \sum_{j=1}^{J} \frac{\left|c'_{ij} - c'_{hj}\right|}{\left(c'_{ij} + c'_{hj}\right)}, \quad (2)$$

where D_{ih} = the distance between species i and h; and
J = the number of columns (vessel-months).

To identify species assemblages, the ordination method of nonmetric multidimensional scaling (NMDS) was applied to the matrix of dissimilarities (Kruskal, 1964). As stated by McCune and Grace (2002), "Nonmetric multidimensional scaling is the most generally effective ordination method for ecological community data and should be the method of choice, unless a specific analytical goal demands another method." NMDS searches for positions of n objects (here, n species) in d dimensions such that dissimilarities in ordination space are close to those of the original space. We extracted the first two dimensions of ordination space (d=2) for graphical presentation.

In addition to ordination, we applied nonhierarchical and agglomerative hierarchical cluster analyses. The nonhierarchical cluster analysis was used to partition species into groups, based on the method of k-medoids, a more robust version of the classical method of k-means (Kaufman and Rousseeuw, 1990). The k-medoids approach attempts to identify k objects from the data set

that best represent all objects. Clusters are created by assigning each object in the data set to its nearest representative (i.e., medoid).

As with any nonhierarchical method, the number of clusters k must be specified *a priori*. We applied a range of values and selected the k most concordant with the data, as quantified by highest average silhouette width. The silhouette width of each species measures its goodness of clustering. For any given k, silhouette widths averaged over species within clusters indicate relative strength of assemblages; across k, the highest average width computed from all species corresponds to the optimal number of clusters (Rousseeuw, 1987). To examine uncertainty in the optimal number, a bootstrap procedure was applied in which columns (vessel-months) of the original data matrices were resampled with replacement to produce n=1000 bootstrapped matrices of the original dimension, and then n=1000 average silhouette widths were recomputed for each k.

The hierarchical cluster analysis was included to provide a comparison with clusters computed by k-medoids and to quantify associations among species, as represented by dendrograms. The hierarchical analysis was based on the linkage method of McQuitty (McCune and Grace, 2002).

Indices of abundance

Indices of abundance were computed to examine synchrony of dynamics among stocks and thus, to investigate the basic assumption that an indicator species could be used to infer dynamics of other species in the assemblage. This investigation focused on the three strongest assemblages (i.e., strongest coherence among members), as measured by average silhouette widths from the cluster analysis. Because the strongest assemblages were examined, this investigation is a best-case scenario. If strongly associated populations do not exhibit synchronous dynamics, one should not assume that weakly associated populations do otherwise.

Ideally, indices of abundance should be computed from fishery independent data; however, for many species here, such data were unavailable or insufficient. In this study, indices were computed from the headboat data set. Fishing effort from headboats is applied generally toward many species, rather than toward specific targets. Because effort is nondirected, any confounding effects of density-dependent catchability are likely to be minimized, and in this regard, headboat data are similar to fishery-independent data.

Indices of abundance were computed from catch and effort data in units of number of fish landed per angler-hour. Data were considered from 1978, the first year of full area coverage, to 2005. For each species, a trip was included only if a species from the relevant assemblage was landed. Thus, many trips were excluded, and some trips were included that had effort but zero catch. This approach represents effective effort more accurately than if all trips were included (a situation that would inflate the assumed effort) or if trips were restricted to those that landed the species in question (a situation that would deflate the assumed effort).

To compute indices of abundance, catch and effort data were standardized using a generalized linear model (Hardin and Hilbe, 2001). The explanatory variables for the model were year, month, and geographic area. To ensure adequate sample sizes by geographic area, sampling areas were aggregated into four regions: North Carolina, South Carolina, Georgia–northern Florida, and southern Florida (south of Cape Canaveral). The response variable was catch per effort, assumed to be distributed with delta-lognormal error structure (Lo et al., 1992; Stefánsson, 1996; Maunder and Punt, 2004). In this structure, the proportion of positive values is modeled with binomial error, and positive values themselves are modeled with lognormal error. Indices were not computed for species that were caught in fewer than 20% of trips on the relevant assemblage, to avoid estimation error associated with inflation of zero values (Lampert, 1992). Because this criterion excludes rarely caught species, evidence of synchrony in our results should be viewed as a necessary but not sufficient condition for the use of indicator species.

Synchrony in dynamics between any two stocks was measured by the Spearman's rank correlation coefficient, computed both from 1) the indices of abundance and 2) the first-differenced time series of log-abundances (z_t):

$$z_t = \log U_t - \log U_{t-1} = \log \frac{U_t}{U_{t-1}}, \quad (3)$$

where U_t = the index value of a stock at time t. Positive correlation of the indices themselves would indicate similar trends in abundance over time. The use of first differences, as in Equation 3, rather than raw or relative abundance, puts emphasis on annual population growth rates and may reduce spurious correlation (Bjørnstad et al., 1999). Positive correlation of growth rates would indicate that stocks not only have similar patterns of productivity (growth, recruitment, and mortality), but that they also respond similarly to interannual variation in fishing effort or catchability.

Significance levels of correlation coefficients were obtained nonparametrically with n=10,000 randomizations of z_t (Prager and Hoenig, 1989; Edgington, 1995; Bjørnstad et al., 1999). A coefficient that ranks sufficiently high in relation to the randomizations could be considered significantly positive, and a coefficient that ranks low, significantly negative. Significance was determined with a two-tailed test at the α=0.1 level with Bonferroni correction.

Results

Species assemblages

Multidimensional scaling did not reveal strongly isolated groups of species in ordination space (Fig. 1). It did, however, reveal consistency of ordination in the sense

that many species had similar neighbors across headboat and commercial data sets. For example, in both data sets, lane snapper was near blue runner, gray snapper, mutton snapper, and yellowtail snapper (see Appendix for scientific names). This repeatability of results provides evidence of species assemblages.

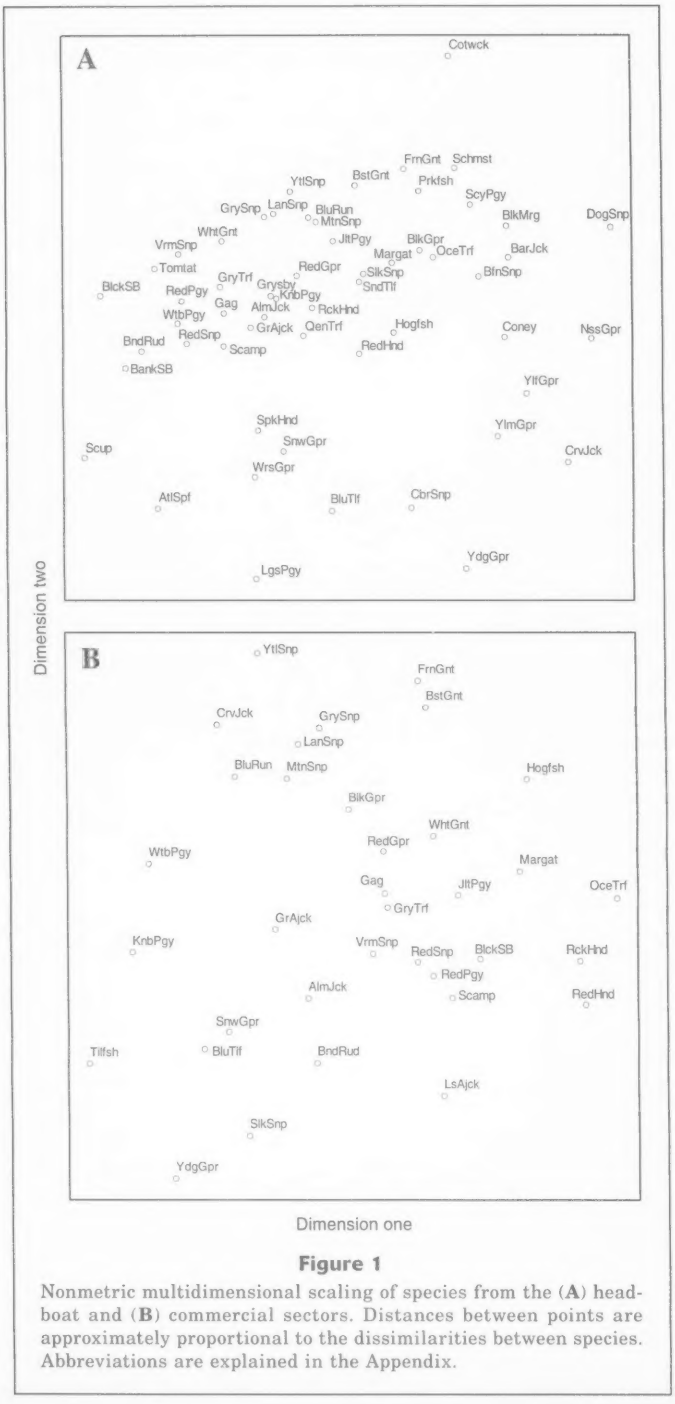

Figure 1

Nonmetric multidimensional scaling of species from the (**A**) headboat and (**B**) commercial sectors. Distances between points are approximately proportional to the dissimilarities between species. Abbreviations are explained in the Appendix.

The k-medoid cluster analyses identified k=14 clusters as most compatible with the headboat data and k=7 clusters as most compatible with the commercial data (Fig. 2). These optimal numbers of clusters were not cleanly defined because peaks in average silhouette widths lacked distinction (Fig. 2). In general, assemblages were similar across data sets, at least for species that were present in both data sets (Table 1).

Hierarchical cluster analyses provided associations among species that were consistent with the assemblages of k-medoid analyses. In hierarchical analysis of the headboat data (Fig. 3), three assemblages had the strongest similarities among member species, labeled here as the deepwater assemblage (blueline tilefish, snowy grouper, speckled hind, and yellowedge grouper), southern assemblage (blue runner, gray snapper, lane snapper, mutton snapper, and yellowtail snapper), and northern assemblage (bank sea bass, black sea bass, knobbed porgy, gag, gray triggerfish, greater amberjack, red porgy, red snapper, scamp, tomtate, vermilion snapper, white grunt, and whitebone porgy). In hierarchical analysis of the commercial data, the same three assemblages were identified with few differences in constituent species (Fig. 4). In both data sets, these assemblages had the strongest coherence among member species, as measured by each cluster's average silhouette width (Table 1). Thus, the deepwater, southern, and northern assemblages were examined further for synchrony in indices of abundance.

Indices of abundance

Although data through 2005 were considered, indices of the deepwater assemblage were derived through 1993, because 1994 began regulations that would have invalidated catch per effort as an index of abundance (i.e., one speckled hind per vessel per trip). Deepwater species that met the criterion of at least 20% positive trips were speckled hind, snowy grouper, and blueline tilefish. All southern species met the 20% positive trip criterion, however small sample sizes of these species north of Cape Canaveral, Florida, necessitated combining geographic areas into two regions: southern Florida and all other areas. Northern species that met the 20% criterion were white grunt, gag, tomtate, black sea bass, vermilion snapper, and gray triggerfish.

In general, indices of abundance were not synchronous (Table 2). Within the deepwater assemblage, snowy grouper was positively but not significantly correlated with blueline tilefish, and neither species was strongly correlated with speckled hind. Within the southern assemblage, correlations between species were mostly negative; however, those between yellowtail, lane, and gray snappers were positive and significant, indicating synchrony in this subset. Within the northern assemblage, about half of the correlations between species were negative, and only the correlation between vermilion snapper and black sea bass was positive and significant. These results offer little evidence of synchrony in population trends within assemblages.

Similarly, first-differenced indices of abundances were out of synchrony (Table 3). Correlations between species were both positive and negative; only one was significantly negative (between snowy grouper and speckled hind), and one was significantly positive (between gray triggerfish and vermilion snapper). These results from first-differenced time series do not support the hypothesis of synchrony in annual population growth rates within assemblages.

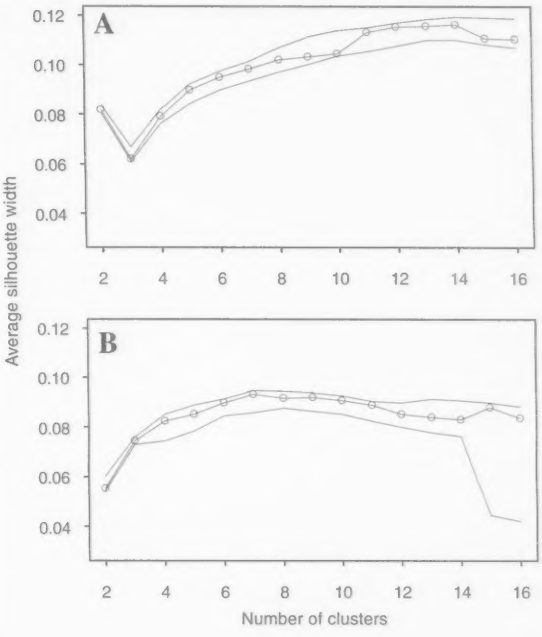

Figure 2

Average silhouette width (lines with circles) from k-medoid cluster analysis of species in (**A**) the headboat sector and (**B**) the commercial sector. Lower and upper lines (without circles) represent 5th and 95th percentiles, respectively, from n=1000 bootstrap replicates. Average silhouette width measures goodness of clustering; higher values indicate better concordance with data.

Discussion

It is unlikely that sufficient resources will ever be available to monitor, assess, and manage every fish stock individually. Thus, managing assemblages by means of indicator species has intuitive appeal. It begins a shift from single-species management toward ecosystem-based approaches and provides a scientific and managerial shortcut by supplanting the need to monitor and assess every managed stock. In the United States, for example, the Magnuson-Stevens Fishery Conservation and Management Reauthorization Act of 2006 (MSRA, 2006) requires that annual catch limits be established to end and prevent overfishing by 2011 in all fisheries (by 2010 for fisheries where overfishing is occurring), yet many stocks cannot be assessed and their status is therefore unknown. Conceivably, setting catch limits by assemblage rather than stock-by-stock could satisfy the statute 1) without substantial new resources devoted to both data collection programs and stock assessment and 2) within the time frame allowed.

Despite its possible appeal, the use of indicator species to extrapolate trends of other species should be viewed with considerable skepticism. From the perspective of niche theory, fishes that coexist are able to do so, in part, because they have adapted to use different niches in their shared environment (May and MacArthur, 1972; Leibold, 1995). Consequently, species within assemblages differ in reproductive characteristics, foraging behavior, habitat requirements, and population-level responses to such factors as competition, predation, disease, and environmental variation (Landres et al., 1988). Because of these differences, population trends of one species (or stock) do not readily extrapolate to others in the assemblage (e.g., Niemi et al., 1997; Shaul et al., 2007). For empirical and theoretical reasons, several authors have concluded that the use of indicator species should be avoided, unless supported by strong evidence from the system in question (Landres et al., 1988; Niemi et al., 1997).

From another perspective, even without strong evidence of synchrony, indicator species may still be useful if applied in a restrictive sense. That is, if fishing effort occurs at the level of assemblages, regulations to reduce effort on one species (the indicator) could transmit to others of unknown status. The cost of this approach would be the forgone yield of any species that could sustain increased rates of exploitation. Ideally, the indicator species should be the weakest link of the assemblage, although defining weakest link could be problematic, along with choosing the correct species (Simberloff, 1998). Furthermore, there may be limited data for the species that is the weakest link of a marine fish assemblage. If achievable, however, such a

Table 1

Clusters of species in headboat and commercial landings, listed in order of strongest to weakest cluster, as measured by each cluster's average silhouette width (in parentheses). Clusters were partitioned around k=14 (headboat) or k=7 (commercial) medoids—values determined by highest average silhouette widths computed from all species. See Appendix for the scientific names of species.

Headboat clusters		Commercial clusters	
One (0.22)	Six (0.07)	One (0.17)	Six (0.01)
Bank sea bass	Cubera snapper	Black sea bass	Bluestriped grunt
Black sea bass	Warsaw grouper	Gag	Crevalle jack
Gag		Gray triggerfish	French grunt
Gray triggerfish	Seven (0.04)	Margate	Lane snapper
Greater amberjack	Blackfin snapper	Red grouper	Whitebone porgy
Knobbed porgy	Cottonwick	Red porgy	
Red porgy	Sand tilefish	Red snapper	Seven (0.00)
Red snapper	Silk snapper	Scamp	Lesser amberjack
Scamp		Vermilion snapper	
Tomtate	Eight (0.03)	White grunt	
Vermilion snapper	Black margate		
White grunt	Coney	Two (0.14)	
Whitebone porgy	Porkfish	Black grouper	
		Blue runner	
Two (0.19)	Nine (0.00)	Gray snapper	
Blue runner	Bar jack	Greater amberjack	
Bluestriped grunt	Black grouper	Mutton snapper	
French grunt	Hogfish	Yellowtail snapper	
Gray snapper	Margate		
Jolthead porgy	Ocean triggerfish	Three (0.07)	
Lane snapper	Red hind	Almaco jack	
Mutton snapper	Saucereye porgy	Banded rudderfish	
Red grouper	Schoolmaster	Blueline tilefish	
Yellowtail snapper		Silk snapper	
	Ten (0.00)	Snowy grouper	
Three (0.18)	Atlantic	Tilefish	
Blueline tilefish	spadefish	Yellowedge grouper	
Snowy grouper			
Speckled hind	Eleven (0.00)	Four (0.04)	
Yellowedge grouper	Crevalle jack	Hogfish	
		Jolthead porgy	
Four (0.11)	Twelve (0.00)	Rock hind	
Almaco jack	Dog snapper		
Banded rudderfish		Five (0.02)	
Graysby	Thirteen (0.00)	Knobbed porgy	
Queen triggerfish	Longspine porgy	Ocean triggerfish	
Rock hind		Red hind	
	Fourteen (0.00)		
Five (0.09)	Scup		
Nassau grouper			
Yellowfin grouper			
Yellowmouth grouper			

restrictive use of indicator species could be considered a precautionary approach to management.

In this study of reef fishes off the southeastern United States, we found little evidence of synchrony in population dynamics, and thus, no support for the use of indicator species. One possible reason for these negative results is that the study area was too broad; however, similar findings have been documented at smaller spatial scales (Parker and Dixon, 1998). A second reason is that the indices of abundance did not accurately

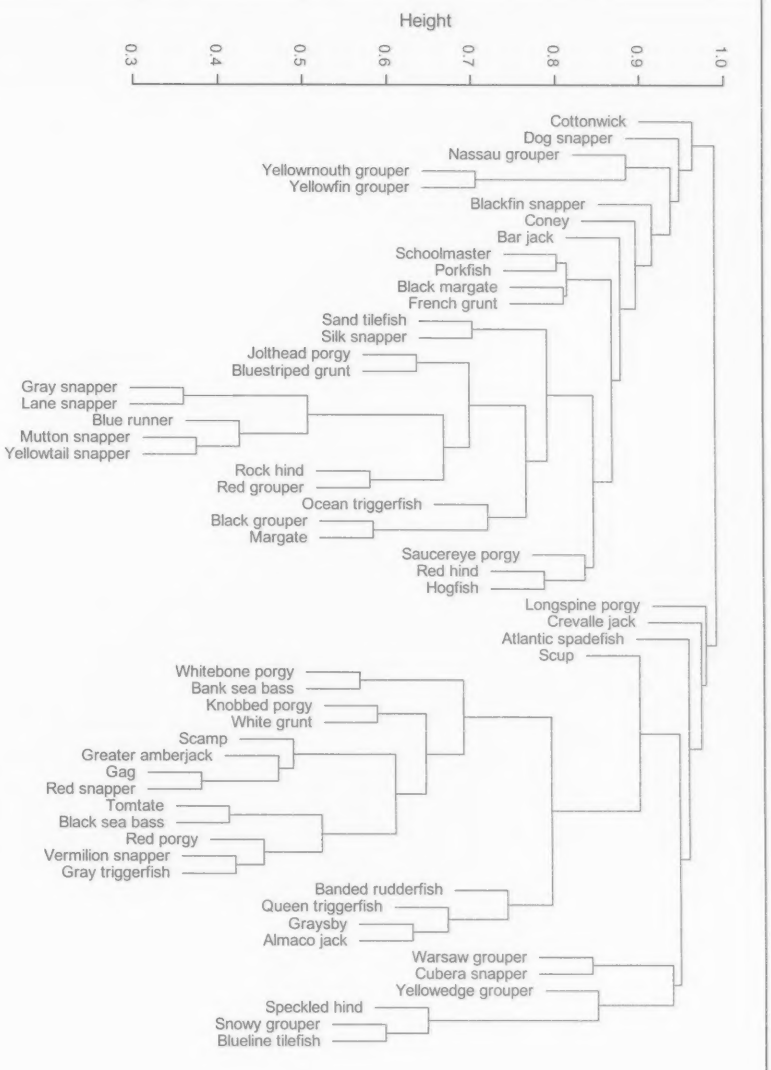

Figure 3

Dendrogram from hierarchical cluster analysis of species in the headboat sector. Height measures similarity among species within a branch, with a value of 1.0 representing the lowest similarity. Scientific names are provided in the Appendix.

represent actual relative abundances because indices were computed from fishery-dependent (headboat) data (Arreguin-Sánchez, 1996; Harley et al., 2001). Fishery-independent data would have been preferable; however, for most species in this study, such data were of small sample size, short survey duration, or were nonexistent. We contend that the headboat data set was the best available for computing indices of abundance because of its relatively large sample size, long duration, and wide geographic coverage. In addition, headboat effort is expended generally toward a complex of species rather than specific stocks, and that generality minimizes any confounding effect of density-dependent catchability. A third possible reason for the negative results is that the population dynamics were truly out of synchrony. From a practical perspective, the actual reason, whether it stemmed from inadequate data or real dynamics, is of secondary concern. Foremost, positive evidence of

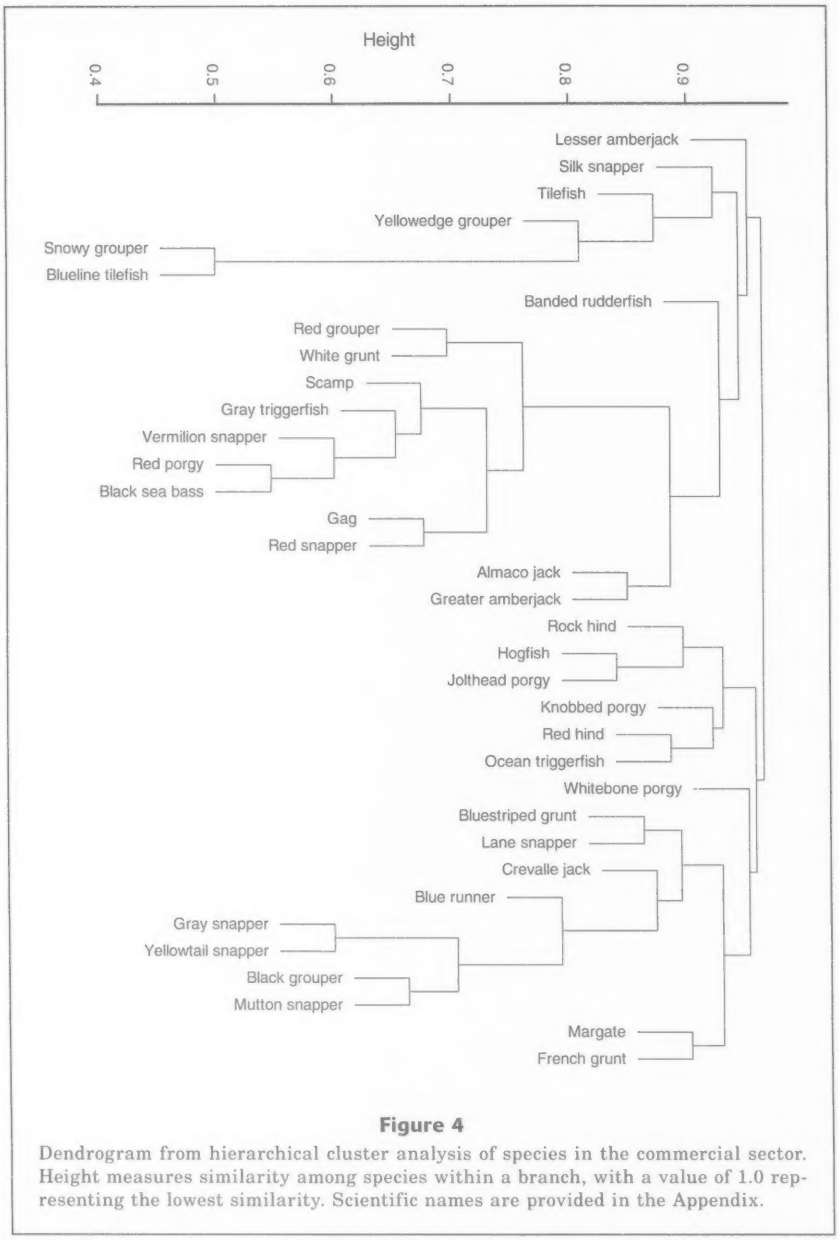

Figure 4

Dendrogram from hierarchical cluster analysis of species in the commercial sector. Height measures similarity among species within a branch, with a value of 1.0 representing the lowest similarity. Scientific names are provided in the Appendix.

synchrony in this reef fish complex has yet to be established, and we therefore urge precaution before using indicator species.

We did find positive evidence of species assemblages on the basis of landings, but these were not necessarily ecological assemblages. Although assemblages in landings may reflect those in nature, the two could differ if some species are preferentially retained from the catch or are more vulnerable to exploitation. Still, assemblages in landings have direct implications from the perspective of managing fisheries, in terms of reducing bycatch and controlling fishing effort across species.

Nondimensional scaling analysis revealed that the species assemblages are not strongly coherent. Such loose structure has also been found in assemblages north of our study area (Mahon et al., 1998). Nonetheless, agreement between the headboat and commer-

Table 2

Synchrony in indices of abundance of reef fishes off the southeastern United States from headboat data. Assemblages are labeled as Deepwater, Southern (south of Cape Canaveral, Florida), and Northern (north of Cape Canaveral, Florida). Values are correlation coefficients and proportions of coefficients (in parentheses) from n=10,000 randomizations that were smaller than the correlations presented, such that values near 1.0 indicate significance of positive coefficients and values near 0.0 indicate significance of negative coefficients. Asterisks note significance at the α=0.1 level after Bonferroni correction (two-tailed test). Abbreviations for species names are explained in the Appendix.

Deepwater	SnwGpr	BluTlf	SpkHnd			
SnwGpr	1.00	0.45 (0.96)	0.08 (0.62)			
BluTlf	—	1.00	−0.06 (0.41)			
SpkHnd	—	—	1.00			
Southern	**BluRun**	**YtlSnp**	**LanSnp**	**GrySnp**	**MtnSnp**	
BluRun	1.00	−0.16 (0.21)	−0.06 (0.38)	−0.11 (0.28)	−0.23 (0.11)	
YtlSnp	—	1.00	0.73*(1.00)	0.78*(1.00)	−0.56*(0.00)	
LanSnp	—	—	1.00	0.82*(1.00)	−0.65*(0.00)	
GrySnp	—	—	—	1.00	−0.64*(0.00)	
MtnSnp	—	—	—	—	1.00	
Northern	**BlckSB**	**WhtGnt**	**Tomtat**	**GryTrf**	**VrmSnp**	**Gag**
BlckSB	1.00	−0.67*(0.00)	0.24 (0.89)	−0.35 (0.04)	0.47*(0.99)	0.37 (0.97)
WhtGnt	—	1.00	−0.41 (0.02)	0.43 (0.99)	−0.35 (0.04)	−0.35 (0.03)
Tomtat	—	—	1.00	0.03 (0.56)	0.36 (0.97)	0.19 (0.83)
GryTrf	—	—	—	1.00	−0.08 (0.34)	−0.14 (0.23)
VrmSnp	—	—	—	—	1.00	−0.04 (0.42)
Gag	—	—	—	—	—	1.00

cial data sets implies that the assemblages, although loosely structured, are not arbitrary. Moreover, additional analyses conducted as part of this study revealed assemblages that were quite similar to those presented. These analyses included the use of an alternative transformation [$\log(x+1)$], alternative measure of distance (binary dissimilarities), alternative linkage method with the hierarchical analysis (average linkage), commercial data from multiday trips (two, three, or four-plus days), and data by trip (i.e., trips not aggregated over months).

The three clusters with the most coherence were deepwater, southern, and northern assemblages. The ranges of these assemblages likely correlate with physical characteristics (as our chosen labels imply). Several of the assemblage species have been found to be linked through latitude, depth, and hard bottom habitat (Sedberry and Van Dolah, 1984; Cuellar et al., 1996). Such information should be beneficial for managing assemblages as units, allowing regulations to be focused on relevant geographic areas.

Although the status of many stocks in the snapper-grouper complex is unknown, it is evident from most stock assessments that overfishing is occurring. In aggregate, these assessment results indicate overfishing of the ecosystem in general (Murawski, 2000). The average level of overfishing and its variance, along with considerations of life histories and vulnerabilities, may indicate appropriate degrees of reduction in fishing effort across assemblages. The use of multiple species as probes into ecosystem health is likely more robust than the use of a single indicator species.

As single-species management loses fashion, its ideal replacement of full ecosystem management remains theoretically appealing, yet impractical given current data and understanding of marine ecosystems. Progress toward ecosystem management will likely occur in increments (Hall and Mainprize, 2004). Where assemblages exist, managing them as such offers a practicable step for implementing ecosystem considerations, including bycatch and species interrelations. Although the results of our study do not support the use of indicator species, they provide information on fish communities fundamental to the judicious application of assemblage management.

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Table 3

Synchrony in first differences of indices of abundance of reef fishes off the southeastern United States from headboat data. Assemblages are labeled as Deepwater, Southern (south of Cape Canaveral, Florida), and Northern (north of Cape Canaveral, Florida). Values are correlation coefficients and proportions of coefficients (in parentheses) from n=10,000 randomizations that were smaller than the correlations presented, such that values near 1.0 indicate significance of positive coefficients and values near 0.0 indicate significance of negative coefficients. Asterisks note significance at the α=0.1 level with Bonferroni correction (two-tailed test). Abbreviations for species names are explained in the Appendix.

Deepwater	SnwGpr	BluTlf	SpkHnd			
SnwGpr	1.00	0.31 (0.87)	−0.61*(0.01)			
BluTlf	—	1.00	−0.14 (0.31)			
SpkHnd	—	—	1.00			
Southern	**BluRun**	**YtlSnp**	**LanSnp**	**GrySnp**	**MtnSnp**	
BluRun	1.00	−0.25(0.11)	−0.10 (0.32)	−0.11 (0.31)	−0.25 (0.11)	
YtlSnp	—	1.00	0.24 (0.89)	−0.08 (0.35)	0.25 (0.90)	
LanSnp	—	—	1.00	−0.19 (0.17)	0.37 (0.97)	
GrySnp	—	—	—	1.00	−0.06 (0.38)	
MtnSnp	—	—	—	—	1.00	
Northern	**BlckSB**	**WhtGnt**	**Tomtat**	**GryTrf**	**VrmSnp**	**Gag**
BlckSB	1.00	0.05 (0.61)	0.16 (0.78)	0.18 (0.82)	0.10 (0.70)	−0.06 (0.38)
WhtGnt	—	1.00	−0.09 (0.33)	0.20 (0.84)	−0.06 (0.37)	−0.22 (0.14)
Tomtat	—	—	1.00	0.08 (0.65)	0.23 (0.88)	0.02 (0.47)
GryTrf	—	—	—	1.00	0.50*(1.00)	−0.11 (0.28)
VrmSnp	—	—	—	—	1.00	0.21 (0.86)
Gag	—	—	—	—	—	1.00

headboat operators who submitted logbook data. The data sets were provided to us by K. Brennan (headboat) and K. McCarthy (commercial).

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Appendix

Species in the snapper-grouper complex off the southeastern United States, as managed under the Snapper Grouper Fishery Management Plan of the South Atlantic Fishery Management Council.

Common name	Scientific name	Short name
Almaco jack	*Seriola rivoliana*	AlmJck
Atlantic spadefish	*Chaetodipterus faber*	AtlSpf
Banded rudderfish	*Seriola zonata*	BndRud
Bank sea bass	*Centropristis ocyurus*	BankSB
Bar jack	*Caranx ruber*	BarJck
Black grouper	*Mycteroperca bonaci*	BlkGpr
Black margate	*Anisotremus surinamensis*	BlkMrg
Black sea bass	*Centropristis striatus*	BlckSB
Black snapper	*Apsilus dentatus*	BlkSnp
Blackfin snapper	*Lutjnaus buccanella*	BfnSnp
Blue runner	*Caranx chysos*	BluRun
Blueline tilefish	*Caulolatilus microps*	BluTlf
Bluestriped grunt	*Haemulon sciurus*	BstGnt
Coney	*Epinephelus fulvus*	Coney
Cottonwick	*Haemulon melanurum*	Cotwck
Crevalle jack	*Caranx hippos*	CrvJck
Cubera snapper	*Lutjanus cyanopterus*	CbrSnp
Dog snapper	*Lutjanus jocu*	DogSnp
French grunt	*Haemulon flavolineatum*	FrnGnt
Gag	*Mycteroperca microlepis*	Gag
Goliath grouper	*Epinephelus itajara*	GolGpr
Grass porgy	*Calamus arctifrons*	GrsPgy
Gray snapper	*Lutjanus griseus*	GrySnp
Gray triggerfish	*Balistes capriscus*	GryTrf
Graysby	*Epinephelus cruentatus*	Grysby
Greater amberjack	*Seriola dummerili*	GrAjck
Hogfish	*Lanchnolaimus maximus*	Hogfsh
Jolthead porgy	*Calamus bajonado*	JltPgy
Knobbed porgy	*Calamus nodosus*	KnbPgy
Lane snapper	*Lutjanus synagris*	LanSnp
Lesser amberjack	*Seriola fasciata*	LsAjck
Longspine porgy	*Stenotomus carprinus*	LgsPgy
Mahogany snapper	*Lutjanus mahogoni*	MhgSnp
Margate	*Haemulon album*	Margat
Misty grouper	*Epinephelus mystacinus*	MstGpr
Mutton snapper	*Lutjanus analis*	MtnSnp
Nassau grouper	*Epinephelus striatus*	NssGpr
Ocean triggerfish	*Canthidermis sufflamen*	OceTrf
Porkfish	*Anisotremus virginicus*	Prkfsh
Puddingwife	*Halichoeres radiatus*	Puddwf
Queen snapper	*Etelis oculatus*	QenSnp
Queen triggerfish	*Balistes vetula*	QenTrf
Red grouper	*Epinephelus morio*	RedGpr
Red hind	*Epinephelus guttatus*	RedHnd
Red porgy	*Pagrus pagrus*	RedPgy
Red snapper	*Lutjanus campechanus*	RedSnp
Rock hind	*Epinephelus adscensionis*	RckHnd
Rock sea bass	*Centropristis philadelphicus*	RockSB
Sailors choice	*Haemulon parrai*	SlsChc
Sand tilefish	*Malacanthus plumieri*	SndTlf
Saucereye porgy	*Calamus calamus*	ScyPgy

continued

Appendix (continued)

Common name	Scientific name	Short name
Scamp	*Mycteroperca phenax*	Scamp
Schoolmaster	*Lutjanus apodus*	Schmst
Scup	*Stenotomus chrysops*	Scup
Sheepshead	*Archosargus probatocephalus*	Shphed
Silk snapper	*Lutjnaus vivanus*	SlkSnp
Smallmouth grunt	*Haemulon chrysargyreum*	SmtGnt
Snowy grouper	*Epinephelus niveatus*	SnwGpr
Spanish grunt	*Haemulon macrostomum*	SpnGnt
Speckled Hind	*Epinephelus drummondhayi*	SpkHnd
Tiger grouper	*Mycteroperca tigris*	TgrGpr
Tilefish	*Lopholatilus chamaeleonticeps*	Tilfsh
Tomtate	*Haemulon aurolineatum*	Tomtat
Vermilion snapper	*Rhomboplites aurorubens*	VrmSnp
Warsaw grouper	*Epinephelus nigritus*	WrsGpr
White grunt	*Haemulon plumieri*	WhtGnt
Whitebone porgy	*Calamus leucosteus*	WtbPgy
Wreckfish	*Polyprion americanus*	Wrkfsh
Yellow jack	*Caranx bartholomaei*	YelJck
Yellowedge grouper	*Epinephelus flavolimbatus*	YdgGpr
Yellowfin grouper	*Mycteroperca venenosa*	YlfGpr
Yellowmouth grouper	*Mycteroperca interstitalis*	YlmGpr
Yellowtail snapper	*Ocyurus chrysurus*	YtlSnp

Spatial and temporal distribution of North Atlantic right whales (*Eubalaena glacialis*) in Cape Cod Bay, and implications for management

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Abstract—Cape Cod Bay (Massachusetts) is the only known winter and early spring feeding area for concentrations of the endangered North Atlantic right whale (*Eubalaena glacialis*) population. During January–May, 1998–2002, 167 aerial surveys were conducted (66,466 km of total survey effort), providing a complete representation of the spatiotemporal distribution of right whales in the bay during winter and spring. A total of 1553 right whales were sighted; some of these sightings were multiple sightings of the same individuals. Right whale distribution and relative abundance patterns were quantified as sightings per unit of effort (SPUE) and partitioned into 103 23-km^2 cells and 12 2-week periods. Significant interannual variations in mean SPUE and timing of SPUE maxima were likely due to physically forced changes in available food resources. The area of greatest SPUE expanded and contracted during the season but its center remained in the eastern bay. Most cells with SPUE>0 were inside the federal critical habitat (CH) and this finding gave evidence of the need for management measures within CH boundaries to reduce anthropogenic mortality from vessel strikes and entanglement. There was significant within-season SPUE variability: low in December–January, increasing to a maximum in late February–early April, and declining to zero in May; and these results provide support for management measures from 1 January–15 May.

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North Atlantic right whales (*Eubalaena glacialis*) have been commercially exploited by whalers for centuries and are listed as endangered under the U.S. Endangered Species Act (ESA). The remnant population of approximately 300 individuals, ranging along continental shelf waters from the southeastern United States to the Scotian Shelf (Winn et al., 1986; Waring et al., 2007), is considered to be a small fraction of its original size (IWC, 2001). Despite a slight increase in the minimum population estimate from 295 individuals in 1992 to 306 in 2001 (Waring et al., 2007), there has been little sign of recovery since studies began in the 1970s (IWC, 2001; Kraus et al., 2001, 2005). Although estimates of survival probability decreased in the 1990s, a relatively modest reduction in mortality rate could reverse the observed decline and reduce the potential for species extinction (Caswell et al., 1999; Fujiwara and Caswell, 2001; Kraus et al., 2005). The most frequent known anthropogenic causes of right whale mortality are collisions with ships and entanglements in fishing gear. Of 50 documented right whale mortalities from 1986 through 2005, at least 19 (38%) were due to ship collisions, and a minimum of six (12%) were attributed directly to entanglements (Kraus et al., 2005).

Cape Cod Bay (Massachusetts), a semi-enclosed basin approximately 40 km in diameter (Fig. 1), is the only known winter and early spring feeding area for the remaining concentrations of the right whale population (Winn et al., 1986; Waring et al., 2007). Scientific observations of right whales in Cape Cod Bay began in 1955 (Watkins and Schevill, 1982; Schevill et al., 1986), and Reeves et al. (1999) reviewed whaling records indicating right whale presence from the early 1600s. During shipboard surveys and commercial whale watching trips, right whales were sighted in Cape Cod Bay and Massachusetts Bay to the north in every month except December from 1978 to 1986. Most of these sightings were sparse for most months, and peak abundance occurred from February through April (Hamilton and Mayo, 1990). With the exception of an unusual summer occupancy in 1986, most right whales had departed

the bays by mid-May (Hamilton and Mayo, 1990). Nearly one third of the population of photographically identified and catalogued individual right whales has been sighted in Cape Cod Bay in recent years (see Hamilton et al., 2007).

To reduce right whale mortality from ship strikes and entanglements, state and federal agencies have enacted a number of management measures. Cape Cod Bay was designated as federal critical habitat under the ESA in 1994 (Federal Register, 1994). The critical habitat includes all of Cape Cod Bay, except the segment of the bay west of 70°30′W, as well as a portion of the waters immediately to the north (Fig. 1), and was defined according to ESA criteria based on the knowledge of right whale distribution and patterns of habitat use available at the time (Hamilton and Mayo, 1990; Federal Register, 1994). In 1997, the state of Massachusetts instituted a Right Whale Conservation Plan that included modifications to fixed-gear fishing practices within state waters and a surveillance-based monitoring program that provided data on right whale presence to mariners and management agencies (Brown et al., 2007). Also enacted in 1997, the federal Atlantic Large Whale Take Reduction Plan (ALWTRP) included measures designed to reduce entanglements in U.S. Atlantic waters (Federal Register, 1997). Regulations under both plans have affected fixed-gear fishing activities in Cape Cod Bay, including those of the lobster trap and anchored sink-gillnet fisheries. The most stringent regulations have been implemented within the boundaries of the critical habitat from 1 January through 15 May. Regulations governing the critical habitat during this period have included a more comprehensive modification of lobster gear than that required from 16 May to 31 December and the prohibition of all gillnetting operations (Federal Register, 2002b). Additional state and federal regulations have been in effect outside the critical habitat, including the seasonal area management (SAM) component of the ALWTRP, which provides additional restrictions on fixed-gear fishing in an area immediately east of the critical habitat (SAM West) from 1 March through 30 April (Fig. 1; Federal Register, 2002a). Although the above are the most relevant spatially and temporally defined management measures, there are several additional and often overlapping regulations affecting fixed-gear fishing in the study area. Ship-strike reduction strategies currently under consideration include measures to reroute ships and to implement speed restrictions from 1 January through 30 April in Cape Cod Bay, as well as speed restrictions in the waters immediately north and east of the critical habitat, or in the proposed Off Race Point Proposed Management Area (Federal Register, 2004, 2006).

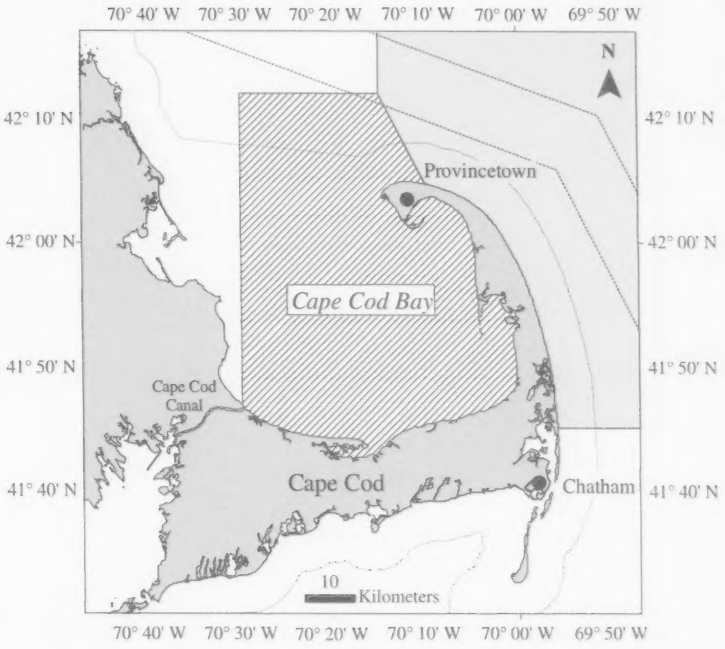

Figure 1

Cape Cod Bay, Massachusetts, including the boundaries of the right whale (*Eubalaena glacialis*) critical habitat (diagonally hatched area), Seasonal Area Management (SAM) West zone (gray shaded area), limit of state-regulated waters (dotted line), and outside boundaries for shipping lanes (dashed lines).

As part of the state conservation plan for right whales, a systematic aerial survey program was implemented in Cape Cod Bay during winter and spring beginning in January of 1998 (Brown et al., 2007). These surveys were designed with an emphasis on detecting right whales and notifying mariners and managers of their presence, and have resulted in a systematic data set that allows right whale occurrence and patterns of habitat use in the bay to be quantified for the first time. The objectives of this study were to use the aerial survey data to describe the spatial and temporal distribution of right whales in Cape Cod Bay, and to compare these data with the extent and timing of present and proposed management measures to evaluate their potential effectiveness. We examined the following critical management strategies: the specification of location and duration for the use of modified fishing gear; the use of critical habitat boundaries as a management unit: and the specification of critical periods when reduced ship speed would be mandated to reduce the mortality of right whales cause by ship strikes.

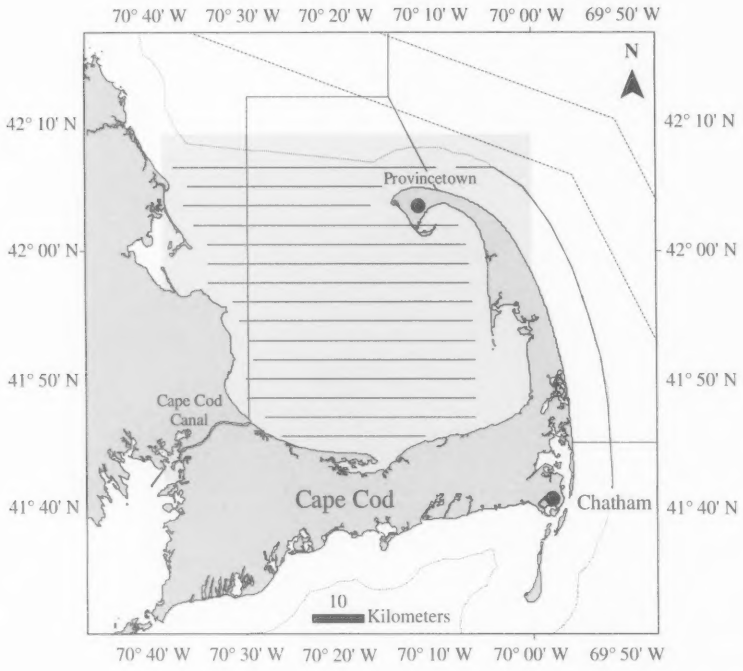

Figure 2

Aerial survey track lines for the Cape Cod Bay right whale (*Eubalaena glacialis*) monitoring program (black lines: 15 east–west lines at 1.5 nautical mile (2.7 km) intervals and a sixteenth line paralleling the eastern shore of the Cape approximately 3 nmi from shore). Also shown are the area boundaries for the sightings per unit-of-effort analysis (shaded gray).

Materials and methods

Aerial surveys

Aerial surveys were conducted from a Cessna 337-A Skymaster, a twin-engine, high wing aircraft with retractable landing gear. The aircraft was flown at a standard altitude of 229 m and a ground speed of approximately 185 km/h, and survey methods were those developed for the Cetacean and Turtle Assessment Program (Scott and Gilbert, 1982) and adapted for right whale surveys (Brown et al., 2007). The aircraft was flown in sea conditions up to and including sea state 4 on the Beaufort wind scale, but were aborted in Beaufort sea state 5 or when visibility decreased below two nautical miles (3.7 km) in fog, rain, or snow.

Surveys were conducted in winter and spring (January through mid-May) of 1998–2002. Additional surveys were conducted in December of some years (for the purpose of this paper, a given year or season includes December of the previous calendar year.) The standard survey design consisted of 16 track lines (Fig. 2). Fifteen east-west track lines were flown at 2.8-km intervals from the mainland to the eastern Cape Cod Bay shoreline. Analysis of the right whale survey data indicated that the effective total survey swath of a Cessna 337 was 4.2 km (Kenney et al., 1995); thus the 2.8 km track line spacing of the standard survey plan was designed to provide 100% coverage of the sea surface in the study area to maximize the potential to detect right whales.

An additional 65-km track line was flown parallel to the outer coast of Cape Cod from the eastern end of the northernmost track line to a point east of Chatham, Massachusetts, at an approximate distance of 5.6 km from shore (Fig. 2). The entire survey (approximately 568 km of track line distance) was completed as often as conditions permitted (ca. 2 surveys/week), and additional track lines to the north of the standard survey design were occasionally added to address management concerns outside the bay (e.g., whale distribution in the shipping lanes).

Analysis of survey data

To quantitatively assess right whale distribution and minimize bias caused by uneven distribution of survey effort, we used the sightings per unit of effort (SPUE)

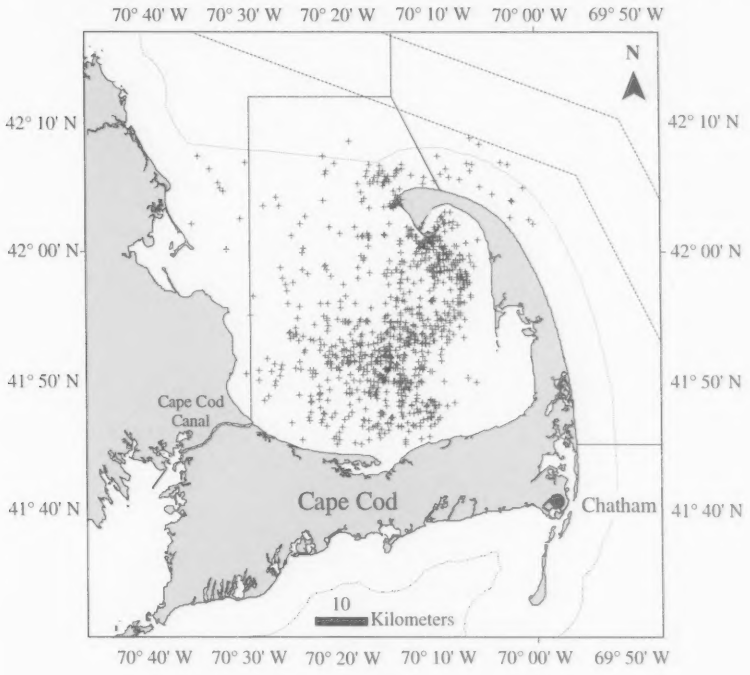

Figure 3

North Atlantic right whale (*Eubalaena glacialis*) sightings (+) recorded during valid aerial survey effort 1998–2002. A sighting is defined as one or more whales observed at the same time and location.

method (Kenney and Winn, 1986). This method first quantifies survey effort as length of track line sampled, then expresses SPUE as the number of whales sighted per standardized length of track.

The boundaries of the study area for this analysis were 42°09′N to 41°39′N and 70°00′W to 70°39′W (Fig. 2). The study area was partitioned into 117 cells measuring 3 minutes of latitude (5.6 km) by 3 minutes of longitude (4.1 km). Each cell was 23 km^2 in area. Fourteen cells lay completely over land and were eliminated; thus there were 103 cells available to be sampled.

Survey data comprised a chronological sequence of latitude and longitude points that described the path flown by the aircraft. Each successive pair of points described a track segment, and the length of that segment (effort) could be computed from the latitude and longitude data (Kenney and Winn, 1986). For each survey, each track segment was partitioned into smaller sections contained within the separate 3-minute cells. In order to standardize effort further, only those segments were completed where visibility was at least 3.7 km, Beaufort sea state was 3 or lower, aircraft altitude was below 325 m, and observers were on watch. Similarly, only right whales sighted under these defined, valid effort conditions were included in our study. We included only sightings identified by observers in the field as definite or probable right whales in the analysis; sightings identified as possible right whales were eliminated. A sighting was defined as one or more whales observed at the same time and location; for simple distribution maps (e.g., Fig. 3) all sightings were treated as single points, but the number of whales sighted is factored into the SPUE analysis. The sampling season was defined as December through mid-May, and was divided for analysis into 12 two-week periods (1 December–17 May). Total effort and total number of right whales sighted within each cell were summed within periods and across years; then the number of whales sighted was divided by effort to generate the SPUE index, in units of whales sighted per 1000 km of valid effort. Cells with less than 2 km of effort (half the width of a cell) within a 2-week period were considered to have been inadequately sampled and were eliminated from further analyses.

For mapping purposes, the SPUE values were ranked into levels. All cells with SPUE>0 were pooled, sorted from highest to lowest SPUE values, and separated by quartiles, representing the top, second highest, third, and bottom quarters of the distribution. The upper quarter was further partitioned by identifying the top 5% of all values. These values were mapped by using different shadings to show the classes. The cells were

Table 1

Total acceptable survey effort (i.e., where visibility was at least 3.7 km, Beaufort sea state was 3 or lower, aircraft altitude was below 325 m, and observers were on watch) for right whales (*Eubalaena glacialis*) in the Cape Cod Bay, Massachusetts, study area, summarized by two-week periods across the entire study, 1998–2002.

Period	Effort (km)
1–14 December	900
15–28 December	550
29 December–11 January	3203
12–25 January	5476
26 January–8 February	8242
9–22 February	7953
23 February–8 March	7535
9–22 March	4983
23 March–5 April	7965
6–19 April	9006
20 April–3 May	7863
4–17 May	2790

Table 2

Mean (±standard error [SE]) and maximum number of sightings of North Atlantic right whales (*Eubalaena glacialis*) per unit of effort (no. of whales/1000 km of survey effort) in Cape Cod Bay, Massachusetts, summarized by year.

Year	Mean	SE	Maximum	*n*
1998	14.58	2.45	789.4	819
1999	11.48	1.49	417.3	874
2000	18.44	2.49	625.7	728
2001	12.74	1.70	575.7	802
2002	2.11	0.61	210.7	739
All	11.91	0.84	789.4	3962

pooled across periods before classification; therefore the maps showing different time periods were comparable. As a test of the definition for critical habitat boundary (i.e., a definition that did not include a potential effort bias), SPUE values were compared between the 3-minute cells inside the critical habitat, outside and west of it (western Cape Cod Bay), and outside and east of it (outside of Cape Cod).

All computations and statistical analyses were performed with Statistical Analysis System procedures (SAS for Windows, vers. 6.13, SAS Inst. Inc., Cary, NC). Calculations of effort and SPUE were performed with custom SAS programs developed at the University of Rhode Island. Whenever possible, we used statistical tests of hypotheses with nonparametric methods (in SAS PROC NPAR1WAY) to avoid the assumptions of normal distributions and homogeneous variances associated with parametric tests. The test most often used was the Kruskal-Wallis nonparametric ANOVA. When the comparison involved only two distributions, the Wilcoxon rank sum test was used (equivalent to the Mann-Whitney *U* test or a parametric *T*-test). The only parametric test that we used was a Duncan's multiple range test (in SAS PROC GLM), which allowed us to perform multiple pairwise *T*-tests while correcting the critical significance probabilities for the number of comparisons. There is no nonparametric test equivalent available in SAS.

Results

During the 1998–2002 seasons, 167 aerial surveys were conducted, yielding 66,466 km of acceptable survey effort. Of the 103 3-minute cells available to be sampled in the study area, 101 (98.1%) were sampled at least once, and 88 (85.4%) were sampled in every year. Because the basic sampling unit represented aggregated data within a cell across a 2-week period, the maximum possible sample size was 6180 (103 cells × 5 years × 12 periods), and the actual number of samples (effort >2 km) was 3962 (64.1% of the maximum possible). Overall mean effort was 658 km of survey track per 3-minute cell (range: 2.5 to 1189.5 km). Spatial distribution of effort was fairly uniform throughout the study area; lowest effort occurred in the peripheral cells, some of which were partially over land. Temporal distribution of effort was relatively consistent during the study period, with the exception of December, when surveys were conducted on an *ad hoc* basis (Table 1). Effort was lower in May than from January through April because surveys in May were suspended after two or three consecutive surveys when right whales were not sighted. The remaining temporal variability in survey effort was primarily due to weather conditions or sea ice that prohibited or shortened surveys.

During the aerial surveys, 1553 right whales were sighted, the majority of which were sighted during February–April. Cumulative sighting totals included multiple sightings of photographically identified individual whales within and between seasons. The earliest sighting within a season occurred on 13 December 1998, and the latest sighting occurred on 2 May 1999. The highest number of right whales sighted on a single day was 47 on both 4 March 1998 and 27 March 2000. Sightings of 203 whales occurred during unacceptable survey conditions (mostly due to high sea state), and eight whales were documented for cells with acceptable conditions but during which there was less than 2 km of effort during a particular 2-week period; therefore sightings of 1342 whales were included in the SPUE analysis. Right whales were sighted during acceptable conditions in 69 of the 101 sampled cells (68.3%) over the five years of the study. Sightings were concen-

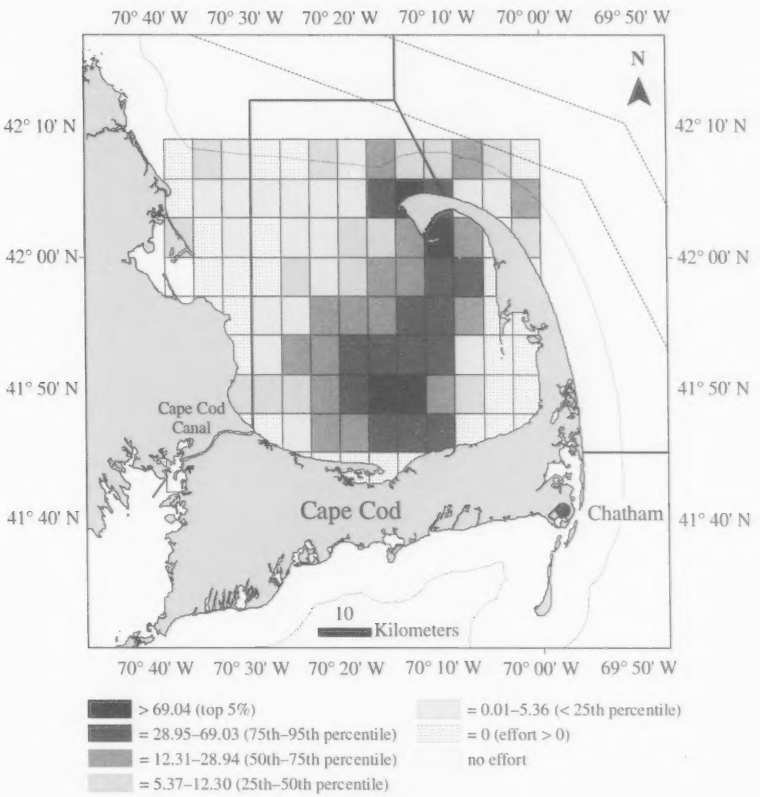

Figure 4

Overall mean North Atlantic right whale (*Eubalaena glacialis*) sightings per unit of effort (SPUE; number of whales/1000 km of survey effort) in Cape Cod Bay, 1998–2002. SPUE values are separated by quartiles, representing the top, second highest, third, and bottom quarters of the distribution. The upper quarter is further partitioned by identifying the top 5% of all values.

trated in a band extending across Cape Cod Bay from the southwest to the northeast (Fig. 3).

The overall 5-year mean SPUE value for all 101 sampled cells was 11.9 whales per 1000 km of survey effort (i.e., one right whale every 84 km of acceptable survey flown; Table 2). The maximum SPUE in a single cell during any two-week period was 789.4 right whales/1000 km (i.e., one whale every 1.3 km) during 29 December 1997–11 January 1998. An area of high-SPUE cells extended along the eastern side of the bay from the south to the tip of the Cape (Fig. 4). Distinct areas of lower SPUE values radiated out from the highest-value cells, and a gradient of decreasing SPUE values extended to the west.

Annual mean SPUE was highest in 2000 and lowest in 2002 (Table 2), and the difference was almost an order of magnitude. The interannual variability was statistically significant (Kruskal-Wallis nonparametric ANOVA, $P<0.001$). When 2002 data was eliminated, the interannual variability remained statistically significant (Kruskal-Wallis, $P=0.033$). When we tested for differences among the annual means with a parametric Duncan's multiple range test, using either unweighted or effort-weighted means, 2002 was found to be significantly different from all other years. Using the unweighted means, we found that 1998 and 2000 were not different from one another, and neither were 1998, 1999, and 2001. Using the effort-weighted means, we found that 1998, 1999, and 2001 did not differ, but that 2000 was significantly different from all other years.

When separated into two-week periods pooled across all years, mean SPUE values varied considerably. SPUE values were low in December and January, increased during February, exhibited two peaks in late February–early March and late March–early April, and declined to low values by the end of April and to zero in May (Table 3). The within-season temporal variability was statistically significant (Kruskal-Wallis, $P<0.001$). The area occupied by right whales expanded and then contracted over the course of the season in

the same fashion (Fig. 5). The center of right whale occurrence tended to remain relatively consistent across the season, and there was no statistically significant variability in mean latitude or longitude (for the 2-week intervals, weighted by SPUE) across the periods (Kruskal-Wallis, P=0.270 for latitude, P=0.580 for longitude). Similarly, there was no significant interannual variability in mean latitude (P=0.063) or mean longitude (P=0.797).

The timing of the SPUE maximum varied markedly between years: late February–early March in 1998, early to mid-April in 1999, late March–early April in 2000, early March to mid-April in 2001, and late February–early March in 2002. This interannual variation was responsible for the apparent bimodal pattern seen over the season when data were pooled across all five years (Table 3). The within-season temporal variation was statistically significant in each of the five years (P<0.001 for each). The duration of right whale occurrence also varied substantially between years: January–April in 1998 (no December 1997 surveys), December–April in 1999, mid-January–mid-April in 2000, and at least late December–mid-April in 2001 (no surveys were undertaken during the first two weeks of December 2000), and only late January–late March (and a second brief period in early April) in 2002. The numbers of consecutive two-week periods when right whales were observed were 9 in 1998, 9 in 1999, 7 in 2000, 9 in 2001, and 5 in 2002.

Approximately 97% of the right whales sighted within the study area by aerial survey were within the critical habitat boundaries (Fig. 3). The critical habitat included approximately 75% of the total ocean area within our defined study area. The majority of cells within which right whales were sighted were inside the critical habitat, but 17 cells with SPUE >0 fell partially or entirely outside the critical habitat (Fig. 4). SPUE did vary significantly among the three areas (Kruskal-Wallis, P=0.009). However, the mean values for the cells east of the critical habitat (11.1 unweighted, 10.9 weighted by effort and by the proportion of cell area for the five cells straddling the eastern boundary) fell between the area inside the critical habitat (18.5 unweighted, 23.1 weighted) and the aa outside to the west (2.3 unweighted, 2.0 weighted). Pairwise nonparametric comparisons (Wilcoxon rank sum tests, weighting was not possible) showed statistically significant differences between the areas east and west of the critical habitat (P=0.023) and between the areas inside and to the west (P=0.003), but not between the areas inside and to the east (P=0.669).

Table 3

Mean (±standard error [SE]) and maximum number of sightings of North Atlantic right whales (*Eubalaena glacialis*) per unit of effort (no. of whales/1000 km of survey effort) in Cape Cod Bay, Massachusetts, summarized by two-week periods across the entire study, 1998–2002.

Period	Mean	SE	Maximum	*n*
1–14 Dec	4.21	3.53	417.3	121
15–28 Dec	4.47	4.47	339.9	76
29 Dec–11 Jan	7.70	2.87	789.4	328
12–25 Jan	4.53	1.34	288.3	378
26 Jan–8 Feb	10.98	2.67	554.4	417
9–22 Feb	14.08	2.40	510.8	407
23 Feb–8 Mar	23.15	4.60	729.8	333
9–22 Mar	14.79	3.14	625.7	395
23 Mar–5 Apr	23.54	3.47	575.7	410
6–19 Apr	14.70	2.51	552.1	412
20 Apr–3 May	6.63	1.67	293.1	380
4–17 May	0.00	0.00	0.0	305

Discussion

The spatial pattern of right whale distribution observed during this study was largely similar to that described by Hamilton and Mayo (1990); most sightings were concentrated toward the eastern side of the bay (Fig. 3). The majority of the data collected by Hamilton and Mayo (1990) was derived from opportunistic sightings recorded by researchers working aboard commercial whale watching vessels departing from Provincetown multiple times per day, bound for Stellwagen Bank to the north of Cape Cod, from mid-spring through early fall. Aerial survey effort in our study was systematic, consistent across years, and spatially uniform throughout the study area and thus provided the first complete representation of the spatial and temporal distribution of right whales in Cape Cod Bay during winter and spring. The SPUE analysis provided a more refined interpretation of raw sighting data than have earlier analyses by reducing bias caused by uneven allocation of effort.

During the seasonal expansion of right whale distribution in the bay (Fig. 5), right whales may be particularly at risk from collisions with ships traveling between the mouth of the Cape Cod Canal at the southwest and ports to the northeast of the bay (Fig. 1; Ward-Geiger et al., 2005). The above risk should be considered when implementing routing measures for shipping traffic. The boundaries of the Cape Cod Bay critical habitat encompassed the areas of highest SPUE values when pooled across all years and periods, and therefore the existing boundaries appear to service as a good management unit. Despite the low number of sightings east of Cape Cod, the area- and effort-weighted statistics indicated that the waters east of the critical habitat may be important habitat for right whales, providing some support for existing fishery management measures in place east of the critical habitat (SAM West; Fig. 1) and the proposed Off Race Point Seasonal Management Area for shipping activity, which includes the portion of SAM West within the boundaries of this analysis (Federal Register, 2006).

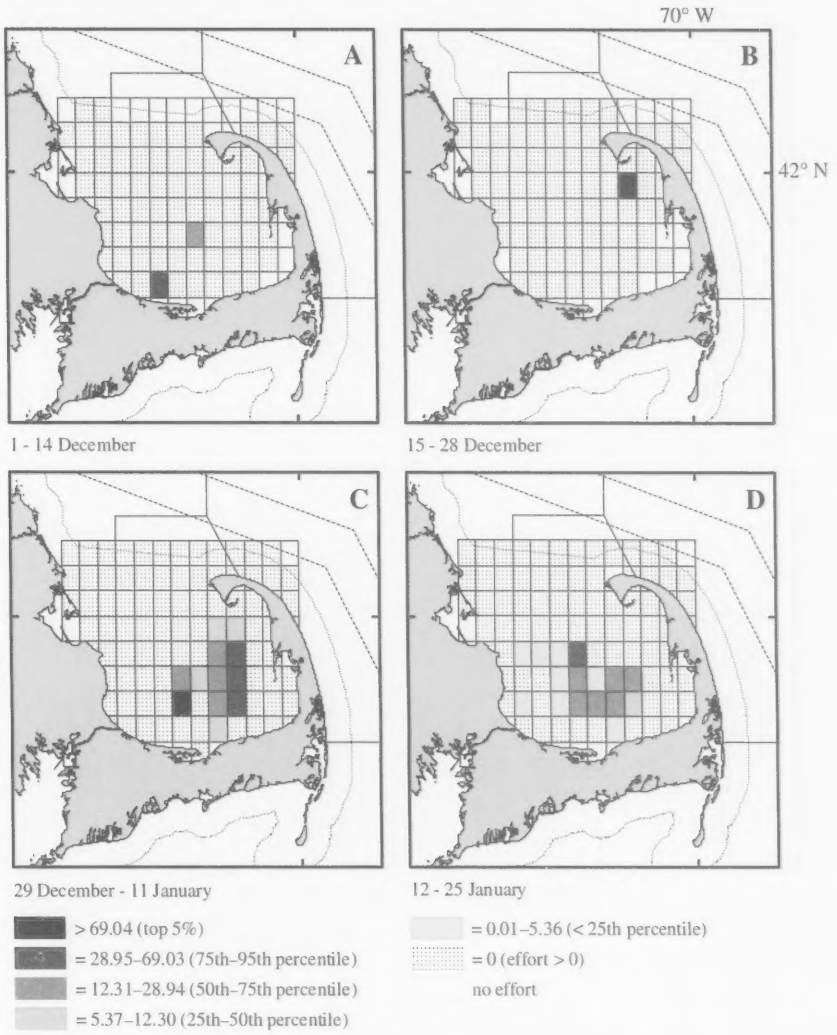

Figure 5

North Atlantic right whale (*Eubalaena glacialis*) sightings per unit effort (SPUE; whales/1000 km of survey effort) in Cape Cod Bay, by two-week period (**A–L**), 1998–2002. SPUE values are separated by quartiles, representing the top, second highest, third, and bottom quarters of the distribution. The upper quarter is further partitioned by identifying the top 5% of all values.

The significant interannual variations in mean SPUE and timing of annual SPUE maxima were likely due to physically forced changes in available food resources. An atypical physical environment and zooplankton assemblage were observed in 2002, compared to 2000 and 2001 (DeLorenzo Costa et al., 2006; Jiang et al., 2007), which corresponded to the order-of-magnitude difference in 2002 right whale SPUE compared to that in 2000. Further comparisons of right whale distributional data and environmental variables should be conducted to assess the causes of the patterns observed. Despite the interannual SPUE variability, the significant within-season and interannual spatial stability of right whale occurrence lends support to the use of these data to define the spatial extent of management measures.

The results of the aerial surveys and SPUE analysis confirmed earlier findings of Hamilton and Mayo (1990) in that peak occurrence of right whales in the study area occurred from February through April. The patterns observed in both studies are largely consistent with earlier, more qualitative descriptions of right whale

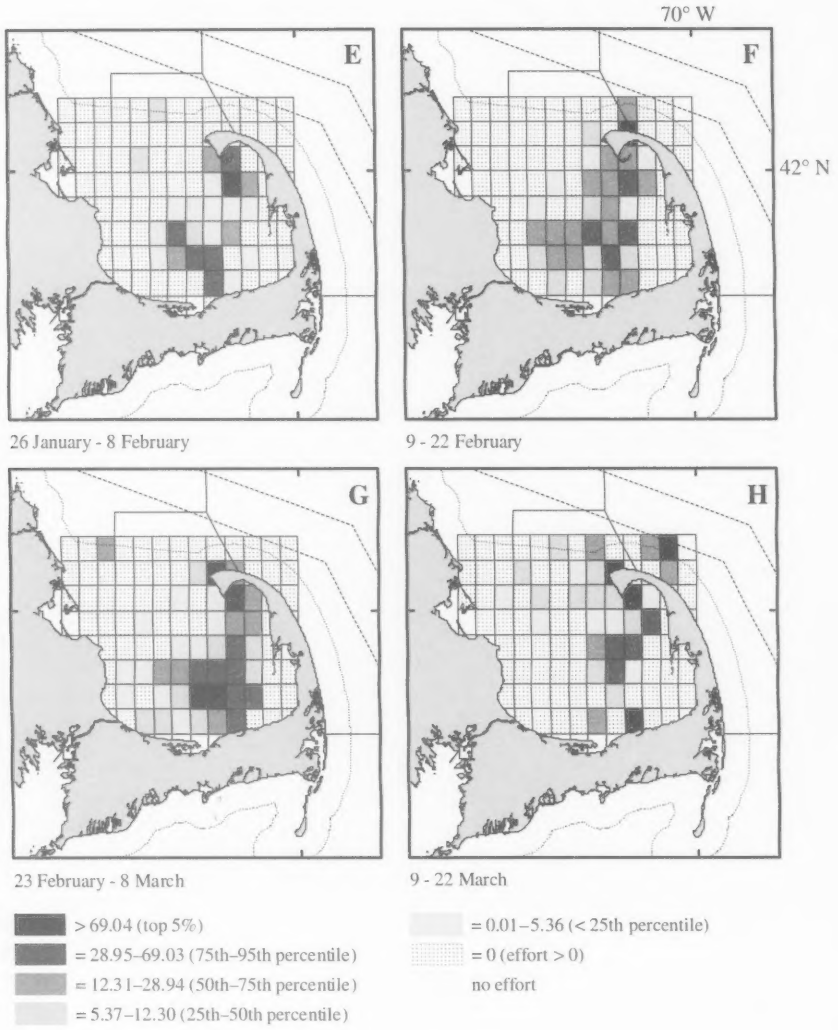

Figure 5 (continued)

occurrence in Cape Cod Bay (Allen, 1916; Watkins and Schevill, 1982; Schevill et al., 1986). More right whales were sighted in December and January of our study than by Hamilton and Mayo (1990); likely a result of the spatial and temporal expansion of survey effort through the surveillance-based monitoring program. The shipboard survey effort of Hamilton and Mayo (1990) was not consistent throughout all the months that were examined in the present study. In the first five years of their eight-year study, there were no surveys in January or February.

Right whales were present inside the critical habitat in December, before the comprehensive gear restrictions were implemented within its boundaries on 1 January, although low December effort makes it difficult to interpret the significance of the sightings. Although gear restrictions were in place through 15 May, no right whales were sighted after 2 May, and SPUE dropped to zero throughout the study area during the period 4–17 May. Moreover, although there were no sightings of right whales after 2 May during our study, there were a few sporadic sightings in the study area throughout May in other years (Hamilton and Mayo, 1990). Given that the period of peak SPUE occurs from February through April, the duration of existing fixed gear fishing regulations (1 Jan–15 May) appears adequate because it provides a buffer of a few weeks on either side of the peak period of right whale abundance—a buffer that allows for the interannual variation observed. The ship-strike reduction measures currently proposed for the period 1 January–30 April (Federal Register, 2004, 2006) should be extended to

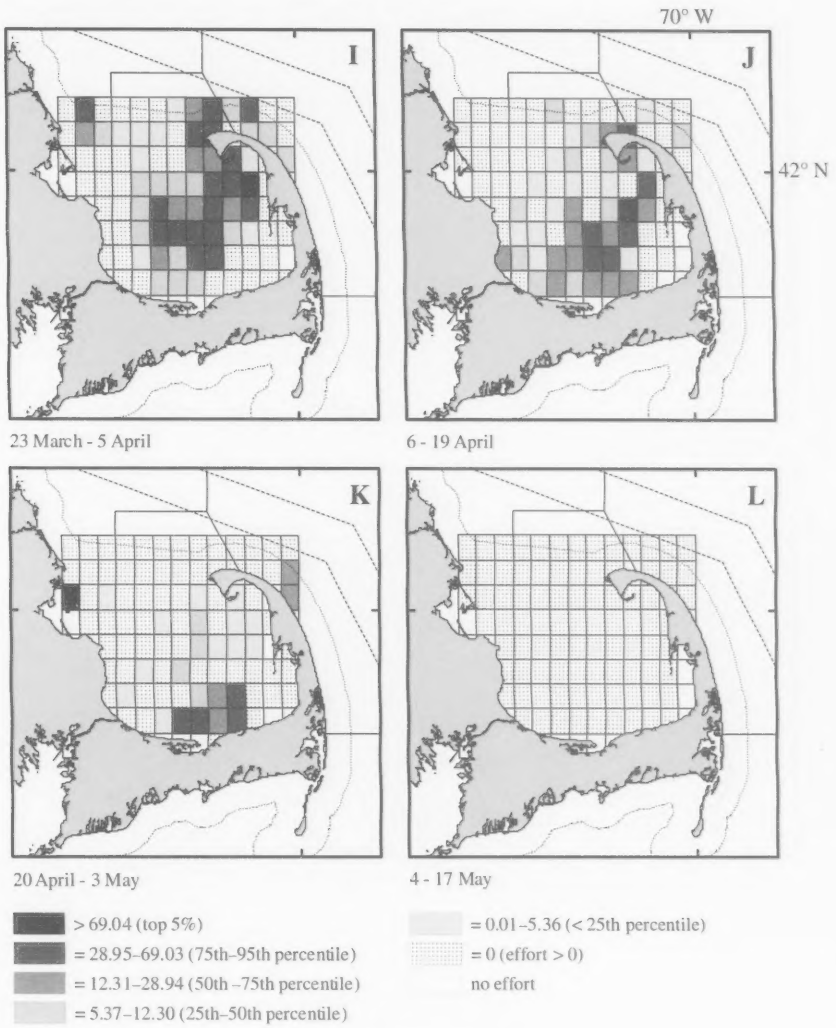

Figure 5 (continued)

15 May to match the duration of fixed-gear fishery restrictions. The efficacy of management measures in Cape Cod Bay has range-wide importance for the right whale because a large portion of the remnant population frequents the bay and because the possibility of even a slight reduction in mortality may prevent species extinction.

Acknowledgments

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Effects of commercial fishing on local abundance of Pacific cod (*Gadus macrocephalus*) in the Bering Sea

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Abstract—Groundfish fisheries in the southeast Bering Sea in Alaska have been constrained in recent years by management measures to protect the endangered Steller sea lion (*Eumetopias jubatus*). There is concern that the present commercial harvest may produce a localized depletion of groundfish that would affect the foraging success of Steller sea lions or other predators. A three-year field experiment was conducted to determine whether an intensive trawl fishery in the southeast Bering Sea created a localized depletion in the abundance of Pacific cod (*Gadus macrocephalus*). This experiment produced strongly negative results; no difference was found in the rate of seasonal change in Pacific cod abundance between stations within a regulatory no-trawl zone and stations in an immediately adjacent trawled area. Corollary studies showed that Pacific cod in the study area were highly mobile and indicated that the geographic scale of Pacific cod movement was larger than the spatial scale used as the basis for current no-trawl zones. The idea of localized depletion is strongly dependent on assumed spatial and temporal scales and contains an implicit assumption that there is a closed local population. The scale of movement of target organisms is critical in determining regional effects of fishery removals.

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As fishery management in the United States moves toward an ecosystem approach, both the direct and indirect effects of commercial harvests on marine food webs are being considered (Schoener, 1993; Murawski, 2000). Localized depletion is the hypothesis that intense fishing pressure may cause small-scale effects on local densities of the target fish—effects that are disproportionate to the managed overall harvest mortality rate. The possibility of localized depletion has been considered in developing and implementing regulations to reduce the jeopardy of mortality of Steller sea lions (*Eumetopias jubatus*) due to fishing in the Bering Sea. In 1997, the western stock of Steller sea lions was listed as endangered under the U.S. Endangered Species Act. Because the period of decline in sea lion numbers coincides with the period of rapid expansion of U.S. domestic fisheries in Alaska (Braham et al., 1980; Hiatt, 2005), there has been concern that commercial fisheries may indirectly affect sea lion abundance through competition for available prey (Alverson, 1992; Fritz et al., 1995).

During their consultations regarding the U.S. Endangered Species Act, scientists of the National Marine Fisheries Service (NMFS) cited the federally managed fishery for Pacific cod (*Gadus macrocephalus*) as one with a potential to adversely affect Steller sea lions. Pacific cod is the third-most valuable commercial fish species in the United States; the value of the 2006 harvest was estimated at $197 million. Approximately 40% of Pacific cod catch is taken by trawling in the southeastern portion of the Bering Sea during the winter "A" season, from 20 January through 31 March (Thompson and Dorn, 2005). The trawl fishery has historically been concentrated on an area of the continental shelf north of Unimak Island, where Pacific cod form dense spawning aggregations during the winter season.

Although the Pacific cod population in the eastern Bering Sea is managed at sustainable overall harvest levels, intensive trawl fishing in a smaller area has been suspected of causing short-term, small-scale impacts on fish abundance (localized depletion) that are disproportionate to the overall harvest rate. Particularly worrisome is the possibility that fishing mortality rates in the heavily trawled area may be much higher than those for the total region, and that this disproportionate mortality may cause reduced availability of Pacific cod as prey for Steller sea lions (Fritz et al., 1995). Evidence indicating such a local effect has been seen in commercial catch data in the eastern Bering Sea (Fritz and Brown, 2005). Under the assumption of reduced prey availability from localized fishing, trawl exclusion zones have been placed around Steller sea lion rookeries and haulouts in western Alaska, and seasonal and spatial allocation of catch quotas have been used to disperse fishing effort. Our goal was to test for effects of localized depletion of Pacific cod caused by the Pacific cod winter trawl fishery.

In order to test for the presence of localized depletion, the temporal and spatial scales of the presumed effects must be specified. Localized depletion is a general term that could encompass several types of interactions. Short-term movement rates of the target species in relation to the scale of the fishery are a critical factor in determining fishing effects. To illustrate, we offer three conjectures on fishery interaction, where the dynamics of harvest and fish movement result in different effects on fish abundance.

For the first conjecture, harvest results in a localized reduction in fish abundance in the immediate vicinity of fishing. This reduction remains geographically stable for some period of time. We refer to this effect as stationary localized depletion. This form of depletion may be envisioned as the action of a dipper to remove certain amount of mud from a bucket; a hole or depression would remain where the mud was removed, eventually filling in but persisting long enough to be observable. Implicit in such stationary localized depletion is the notion that movement by the fish is on a scale smaller than that of the fishery; therefore it does not obscure the geographic imprint of the removal.

For the second conjecture, the movement of the fish interacts with a locally intense harvest. In this case, short-term fish movement occurs on a geographic scale greater than that of the fishery and the effect of the removal would quickly dissipate over the area occupied by the fish. This form of depletion would more closely resemble the action of ladle in dipping water out of a bucket, with no persistent depression left behind by the ladle. On the scale of the ladle, the effect is transitory and there is no apparent localized depletion, even though there is a measurable removal on the scale of the bucket.

For the third conjecture, the short-term fish movement includes a net flow in one direction. In this scenario, fishing effects would show as a change to the flow of fish or as an area of reduced abundance that is displaced downstream. This effect would be similar to intercepting part of a flowing stream with a dip net. Combinations of random and directed short-term movement may also produce effects that are both dispersed and spatially displaced from the location of harvest.

In the specific case of Bering Sea Pacific cod, the scale of fishery harvest is known from commercial fishing data, but the scale of Pacific cod movement is poorly understood. From an early tagging study (Shimada and Kimura, 1994), it was found that Pacific cod make large-scale movements over the eastern Bering Sea on a seasonal basis. Short-term movement dynamics of Pacific cod, on the other hand, are only beginning to be studied (Nichol and Chilton, 2006). Assumed scales of Steller sea lion foraging are based largely on satellite tagging studies of adult female and juvenile Steller sea lions (Merrick and Loughlin, 1997). Measures enacted to protect Steller sea lions include trawl exclusion zones 18.5 or 37.0 km in diameter around Steller sea lion haulouts and rookeries. Use of trawl exclusion zones to reduce competition between Steller sea lions and trawlers implies an assumption of stationary localized depletion at this scale. Thus, under the current regulatory framework, the general question of whether fishing causes some form of localized depletion becomes much more specific, namely that of whether or not trawling causes a stationary localized depletion on the geographic scale of the trawl exclusion zones. Our experiment was therefore designed to address the specific mechanism that causes stationary localized depletion, and we assumed that this type of depletion would have the greatest potential for negatively affecting Steller sea lion abundance.

Materials and methods

Study area

The study area was located in the southeast Bering Sea near the tip of the Alaska Peninsula (Fig. 1)—an area situated off Unimak Island at Cape Sarichef on the eastern side of Unimak Pass, at depths of approximately 70 to 110 m. This area is one of the most productive trawling grounds in the Bering Sea, where fisheries focus a great deal of trawling effort for Pacific cod. The trawl exclusion zone around the Steller sea lion haulout at Cape Sarichef intersects this preferred trawling ground and the two areas provided us an opportunity to use a spatially adjacent treatment zone and control zone. The spatial scale of the experiment was determined by the 18.5-km boundary of the Cape Sarichef trawl exclusion zone and the extent of preferred depths for trawl fishing. The temporal scale, the length of time an effect must persist to be observable, was taken to be approximately two weeks, which was the time required to conduct each phase of the research fishing.

Research pot gear

We used the catch of standardized pot gear as an index of local Pacific cod abundance. Pot gear is widely used in commercial fishing for both crab and Pacific cod in the eastern Bering Sea and Gulf of Alaska. Research catches were based on catch from pots, even though the fishery effect being tested for would have been due to trawling, because pots provide large sample sizes and can be deployed at a very high spatial resolution. Pot catches cannot be easily or reliably used to estimate absolute abundance of fish, but provide a consistent index of relative abundance that can be used to make statistical comparisons between different survey areas or times.

Commercial pots were used during initial feasibility and pilot studies for this project; a standardized research pot was then developed and used for the experiment. The research pots were slightly larger than most commercial pots, and had a smaller net mesh and modified tunnel openings: they were 2.3 m by 2.3 m by 1.2 m, and had 5-cm stretched mesh and two entrance tunnels, each with 68-cm by 23-cm tunnel openings.

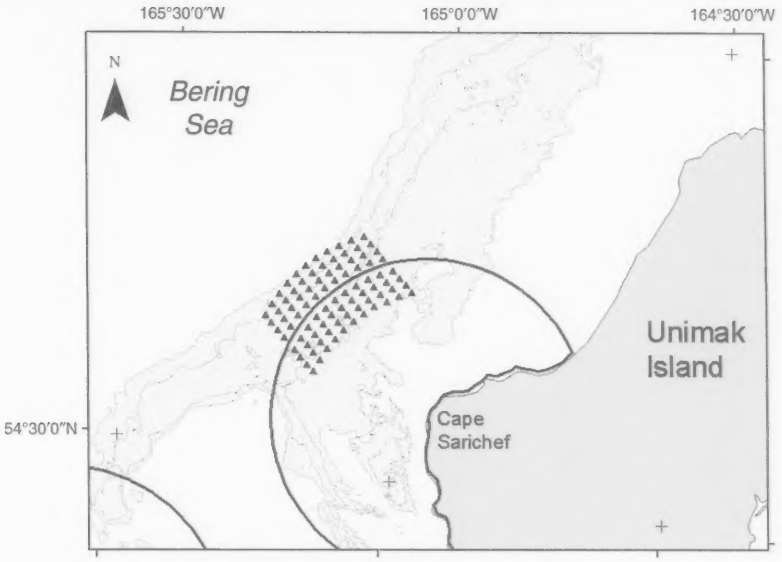

Figure 1

Location of the study to determine localized depletion of Pacific cod (*Gadus macrocephalus*) in the southeast Bering Sea. The large arc shows the regulatory notrawl zone around the Steller sea lion (*Eumetopias jubatus*) haulout at Cape Sarichef on Unimak Island. The small triangles indicate station locations for the experiment. Depth contour lines and light shading show the region of 70 to 100 m depth.

At the tunnel openings there was a modified Hilti-style stainless-steel trigger, a variation of a fish retention mechanism commonly used in cod-pot fishing. Research pots were fished individually with buoy lines, buoy configurations, and other tackle configured similarly to that deployed in commercial pot fishing.

Experimental design

We used an experimental design similar to the class of designs referred to as "before/after control/impact" (BACI). The capabilities and limitations of BACI study designs have been discussed extensively in the ecological literature (e.g., Osenberg and Schmitt, 1994; Hewitt et al., 2001). We used many of the components of a BACI design, but the final design differed substantially from the paired designs of Stewart-Oaten et al. (1992). In our study, the measured quantity was not the difference between treatment and control stations replicated over time, but the percentage difference over time at each station, replicated over space. In this sense, our design was similar to the ANOVA-type designs of Underwood (1994). Our design allowed for expected seasonal and small-scale spatial variability in fish abundance, and provided the necessary replication for hypothesis testing.

The experiment was conducted in 2003, 2004, and 2005. In each year, data were collected during two separate cruise legs: in early January (before the trawling season) and immediately after the main trawl harvest in late March. Sampling was balanced between a treatment area subject to intensive trawl fishing and a control area inside the Cape Sarichef notrawl zone. A total of 80 sampling stations were set along 10 parallel transects intersecting the notrawl zone boundary, and each transect contained four stations inside and four outside the boundary (Fig. 1). Although it was not possible to match treatment and control stations exactly with respect to depth, habitat, bottom currents, etc., this layout provided a similar range of habitats within the two zones.

The quantity of interest for each station was the ratio of the mean pot catch (in numbers or weight of Pacific cod) at that station during the March survey ($\bar{X}_{After}$) to the average catch during the January survey ($\bar{X}_{Before}$). This ratio reflects the percentage change in abundance between the two surveys at a particular station. The seasonal percentage change is referred to as the delta (δ) for the station:

$$\delta = \left(\bar{X}_{After} - \bar{X}_{Before}\right) \Big/ \bar{X}_{Before} = \frac{\bar{X}_{After}}{\bar{X}_{Before}} - 1.$$

The ratio is expressed so that δ will be near zero if the catch is the same at a given station during both the before and after surveys, positive if the catch increases,

and negative if catch decreases over the season. For example, a δ of –0.50 represents a 50% decrease in catch, and a δ of +1.00 represents a 100% increase.

Sampling considerations and gear deployment

There are two important concerns in using catch from fixed-gear such as pots as an index of fish abundance. The relationship between catch and abundance can break down at either very low or very high fish densities (Hubert, 1996). During our pilot studies, soak times and sampling procedures were developed to ensure that the research fishing did not result in either excessive numbers of empty pots or gear saturation (where the number of fish in the pot became so high that catchability of additional fish was reduced). To guard against gear saturation and to provide detail on the timing of fish catch within the soak period, instruments referred to as trigger timers were developed. These instruments involved a magnetic reed switch mounted on the triggers of the pot and an electronic event timer that recorded when the triggers were pushed open. A modular trigger assembly allowed instruments to be mounted and dismounted in pots without slowing down the pace of fishing.

In order to avoid gear saturation and to increase the number of observations, pot soak times were initially kept short (4–8 h), and fishing was conducted mainly during daylight hours. It was not feasible to fully standardize the soak time or the timing of the launch within the diel and tidal cycles over the 40–50 pots fished each day. In order to compensate for variation from these sources, each day's sampling included approximately equal numbers of stations inside and outside the notrawl zone. Difficulty in retrieving pots during strong tidal currents led to a change in procedure between 2004 and 2005. In 2005 a slightly longer overnight soak was used, with pots being launched at new locations in the afternoon or evening and retrieved the next morning.

Results of a pilot study conducted in 2002 showed short-term temporal variation (day-to-day variability in catch rates at a given station) as a larger component of variability than small-scale spatial variation (variability in catch between stations). In order to smooth over short-term temporal variation, we attempted to fish each station on at least three different days during each survey. Each day's fishing was balanced with stations in both the treatment and control areas, so that any short-term influences on abundance would affect both treatment and control groups. The goal was to apply fishing methods in such a way that variation in catch due to soak time, diel and tidal cycles, weather, and current patterns would be minimized and distributed evenly between trawled and untrawled areas.

Our pilot study results also indicated that pots located at least 0.11 km apart functioned as independent sampling units (no correlation between catch for pairs of pots at 0.11 km or further distances). Stations for the experiment were spaced 0.11 km apart within each zone (trawled or untrawled), and 1.8 km apart across the notrawl zone boundary. The same layout of study stations was used for all three years. Examination of both pilot study data and pot fishing data collected by fisheries observers indicated that there was not a strong relationship between length of pot soak and catch over a time span of 4–24 hours. For this reason, catch rates were expressed not as CPUE in fish/hour, but simply as total number or weight of Pacific cod caught per standardized pot deployment. The catch measure at each station was the average catch over all of the days that a station was fished during a survey. The use of an average over several days as the measure at each station provided smoothing over day-to-day variation and reduced the likelihood of zero catches in the final data set.

Pots were baited with chopped Pacific herring (*Clupea pallasi*) contained in meshed bait bags. Bait for each cruise was purchased as a bulk lot so that the same lot of bait was used for the entire cruise. Filled bait bags were weighed and the amount of bait adjusted to within 0.1 kg of the target weight of 5.0 kg. Procedures for securing bait bags and triggers, launching, and retrieving pots were consistent in all cruises.

Upon retrieval, all catch was sorted, identified, and weighed. A systematic subsample of pots (every second, third, or fourth pot retrieved) was selected with a random starting point each day; all Pacific cod from selected pots were processed for length frequency, by sex. The sampling interval was adjusted according to average catch rates so that at least 100 fish were measured each day. The condition of the gonad of measured fish was also examined visually and coded according to a 5-stage system, in order to record the approximate frequency of different stages of reproductive maturity of Pacific cod in the catch

Data analysis

After every study year, average catch rates for each station and cruise were calculated for all valid fishing days at a station. Average catches from the two cruises were used to compute the δ for each station. Spatial mapping of both raw catch data and δs was performed to look for spatial patterns and verify the assumption of independence between study stations. Distance-based correlograms (both anisotropic and isotropic) were plotted to check for spatial dependence in catch data.

Linear models were also used to look for patterns in untransformed catch data; effects of year, season, treatment versus control, station, and fishing day within each cruise were examined. After examination of the distributional characteristics and independence of the δ's, the nonparametric, rank-based Wilcoxon rank sum test (Ott, 1984) was used to test for a difference in distribution of δ between stations in the trawled and untrawled areas. The nonparametric test was selected over the parametric t-test because δ is a ratio of counts and may have a strongly non-normal statistical distribution. All modeling was conducted in S-Plus (Math Soft Inc., Seattle WA; Venables and Ripley, 2002).

Bootstrap methods (Manly, 1991) were used to evaluate the power of the experimental design to correctly identify the presence of a fishing effect. For each study year, daily catch data from all stations and days were pooled for use as a sampling population. Random samples the same size as those used in each year's experiment were drawn. Half of the simulated sample stations were randomly assigned to the treatment group, and the mean catch for these stations in the March cruise was decreased by a fixed percentage to simulate a known fishing effect. Percentage changes were then calculated for each station, and we used the Wilcoxon rank sum test to compare stations in treatment and control groups. This algorithm was repeated 1000 times for each level of fishing effect. The *P*-values computed for each sample were used to compute probabilities of rejecting the null hypothesis for $\alpha = 0.05$, 0.1, and 0.2 for each of the levels of sampling effort.

To check that substantial removals of Pacific cod took place during the study, we evaluated the harvest in the study area using NMFS catch estimates and haul-specific data collected by the Alaska Fisheries Science Center observer program. Winter-season Pacific cod catch for trawl gear was summarized for each of the two federal reporting areas that intersect the study area. These totals included both catches in the study area and catches in other parts of the reporting area. Observer data did not cover all hauls on all vessels but were recorded with spatial precision to the nearest minute latitude and longitude. Records for all observed hauls within the two reporting areas were extracted, and hauls within a one-degree longitude by 30-minute latitude block around the study area were identified. The proportion of observed hauls and total fishing effort (duration of haul) in the study area as a proportion of observed hauls in each reporting area was calculated. The total catch of Pacific cod was determined from the smaller subset of observed hauls (for which there were catch composition data), and the proportion of Pacific cod catch coming from the study area was also estimated. This fraction was then applied to the total catch for the reporting area to obtain a rough estimate of Pacific cod harvested from the study area by gear type.

Tagging studies

In conjunction with the localized depletion study, we conducted studies on the feasibility of determining on Pacific cod movements through tagging. Partial results of these studies are reported here to explain the results of the main experiment. Tagging work included development of methods 1) for capturing and handling Pacific cod with pot gear, 2) for tagging fish and determining data formats, 3) for releasing Pacific cod tagged with archival data-storage tags and standard spaghetti tags, and 4) for studying preliminary tag-induced mortality. The goal of this effort was to collect information on both seasonal migration patterns and small-scale movements of Pacific cod during the spawning season.

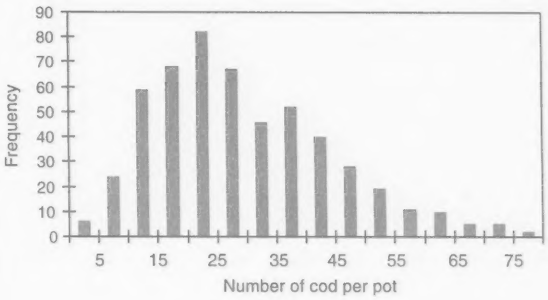

Figure 2

Example of the frequency distribution of pot catch data for Pacific cod (*Gadus macrocephalus*). Catch data are in numbers of fish per pot from all stations during the March 2004 cruise.

An understanding of these movements is important for the interpretation of the local abundance study. During a special tagging cruise in February 2003, tagged fish were released at a series of locations, including within the notrawl zone off Cape Sarichef. Tag recapture was conducted entirely by the fishing industry. Date and location of the recaptures were provided by fishermen and fishery observers. In total, 295 archival tags and over 6000 spaghetti tags were released between 2002 and 2004. Approximately 35% of both types of tags were returned over the five years after tag release. Full results of these tagging studies will be presented in a separate publication.

Results

Field data confirmed that assumptions for the experimental design were met. The frequency distribution of the raw catch data (Fig. 2) illustrated the properties of pot catch. Similar results were obtained with either numbers or weight of Pacific cod per pot as the measured quantity. Zero catches (empty pots) were rare, and there was no evidence of gear saturation at high catches (the upper tail of Fig. 2 declines gradually without a sharp cutoff). Although the distribution of pot catch data was slightly skewed, the skewness and heteroscedasticity were much smaller than is typical for many types of fishery data.

The level of Pacific cod catch varied strongly between study years and seasons but was fairly consistent within each study cruise. Average catch ranged from 8.8 Pacific cod per pot (27.7 kg) in March 2003 to 31.7 cod per pot (105.5 kg) in March 2004. Coefficients of variation for the raw catch data ranged from 64% for January 2004 to 42% for March 2005. Coefficients of variation for cruise averages at individual stations ranged from 14% to 43%. The average catch rate changed substantially between January and March in each year of the study,

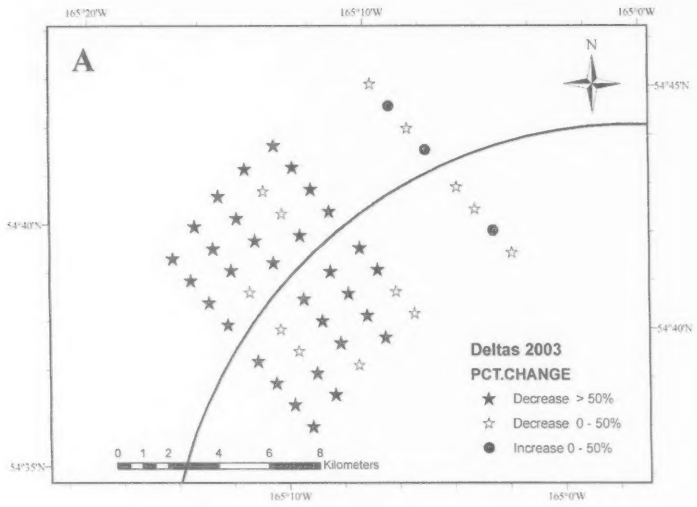

Figure 3

Spatial pattern in seasonal percent change (δ) for the three study years. Refer to Figure 1 for general location of the study area. Symbols show study stations. The arc in the middle of the stations is the Cape Sarichef notrawl zone boundary. Symbol shape and size indicate the size of the percent change in Pacific cod (*Gadus macrocephalus*) catch between "before" (early January) and "after" (immediately after the main trawl harvest in late March) surveys in each year: (**A**) 2003, (**B**) 2004, and (**C**) 2005.

but not always in the same direction. In 2003, the average catch rate decreased 55% from January to March, and nearly all of the individual station changes (δ) were less than 1.0. In 2004 and 2005, the average catch rate increased by 73% and 26%, respectively, from January to March. These differences were presumably the result of interannual differences in the timing of seasonal migration and spawning aggregation

A check of spatial pattern in the raw data and final δ's verified the independence of the experimental study stations and the absence of any strong spatial patterns. There was no consistent spatial pattern in raw catch data, either between trawled and untrawled areas or from southwest to northeast within the study area. There was some evidence of serial correlation between adjacent pots within each fishing day; we believe this correlation to be a result of similarities in timing of pot launches within tidal and diel cycles rather than spatial correlation in fish abundance. There was no spatial correlation in the calculated average catch at each station over a cruise. Although there was some evidence of serial correlation between days within a cruise, averaging the catch at each station over the days within a cruise eliminates this correlation. Maps of percentage change values (δ) also showed no discernible spatial pattern (Fig. 3). Distance-based variograms (both isotropic or anisotropic) were reviewed for the final δ's and we found no significant spatial correlation as a function of distance between pots. Correlation of pairs of δ's at all distances of 0.11 km or more were not significant, verifying the assumption of independence between stations.

Implementation of the study design was generally successful, and good replication was obtained. The exception was the January cruise in the first year of the experiment (2003), where severe weather and mechanical problems severely curtailed the field effort. Sample size from this cruise (160 pots fished) was small (Table 1). The March "after" cruise in 2003 was, however, successful; a total of 475 pots were fished and full replication at all 80 experimental stations was obtained. Both before and after cruises in 2004 and 2005 achieved full coverage of the 80 stations and good replication. Because of the very low sample size in January 2003, δ's could be calculated for only 48 of the study stations, and some before values were based on only a single measurement. In 2004 and 2005, δ's at all 80 study stations were calculated from the averages for over three to five replicate fishing days within each cruise. The resulting values ranged from negative numbers, representing a net seasonal decrease at a station, to fairly large positive values, indicating a substantial seasonal increase. In 2004, there was a particularly large outlier (δ>4) at one station which had very low catches in January. The shift to overnight soaks in 2005 resulted in not only smaller variance of the raw catch data but in smaller

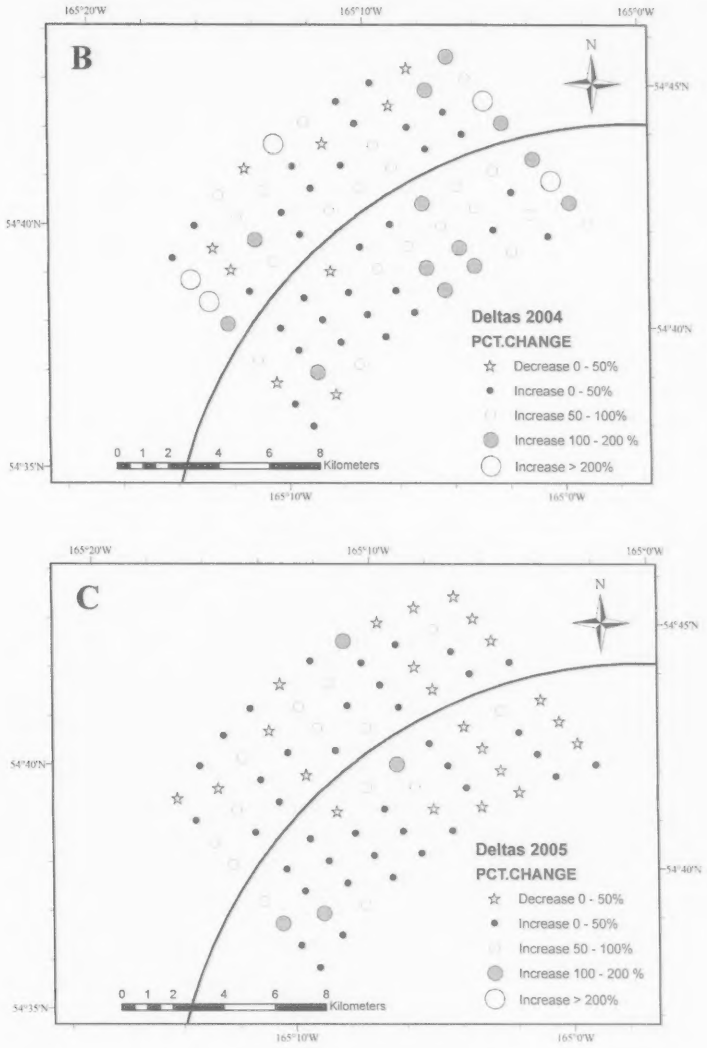

Figure 3 (continued)

variance of the δ's. Although the small sample size in January 2003 limited the power of statistical testing in this year, the overall consistency of the results persuaded us to include the 2003 data set in final analyses.

Analysis of the raw data foreshadowed the overall results of the study. We examined the catch data from individual pots, using standard linear model analysis. The best-fit linear model accounted for only 30% of the variability in the data, reflecting the importance of other sources of variability not included in the model. The treatment effect (trawled vs. untrawled zone) was not significant for the raw data, indicating only slight differences in baseline abundance between the two zones. The interaction term for treatment and season (which is the term that would reflect a substantial localized depletion in the trawled zone) was strongly not significant. As pointed out in discussions of simple BACI analysis (Hurlbert, 1984; Stewart-Oaten et al., 1986; Underwood, 1991), the interaction term from the standard ANOVA does not provide the correct error term for a true test of impact; for testing the presence or absence of localized depletion we used the analysis of δ's.

Final results of the study clearly indicated very similar values of seasonal change in Pacific cod abundance (δ) in both the trawled and untrawled portions of the study area. We did not see the differences in slope that we would have expected to result from strong localized depletion in the trawled zone. When we used the rank-based Wilcoxon test to look for differences in mean δ between the trawled and untrawled regions, *P*-values

Table 1

Dates and summary statistics for cruises conducted during the Bering Sea localized depletion experiment for Pacific cod (*Gadus macrocephalus*). Each year's experiment included a "before" cruise in early January (before the trawling season) and an "after" cruise in late March immediately after the main trawl harvest.

Cruise dates	Cruise purpose	Number of days fishing	Number of pots fished	Average number of cod/pot	Average weight (kg) of cod/pot
30 Mar–25 Apr 2002	Pilot study and tagging	21	703	28.8	103.4
28 Dec 2002–8 Jan 2003	Abundance experiment—before	4	160	22.2	104.4
4–17 Feb 2003	Tagging	11	336	22.3	78.3
12–31 Mar 2003	Abundance experiment—after	14	475	8.8	27.7
2–10 Jan 2004	Abundance experiment—before	9	360	19.3	93.3
15–31Mar 2004	Abundance experiment—after	15	604	31.7	105.5
9–22 Mar 2005	Abundance experiment—before	14	481	21.2	85.3
16–29 Mar 2005	Abundance experiment—after	14	500	25.7	95.4

for the three study years were 0.70, 0.92, and 0.81, respectively. Although the range and mode of the observed δ's changed from year to year, in each year the distribution of δ's over stations within the two zones was very similar (Fig. 4).

Power simulations gave us confidence that the strong failure to reject the null hypothesis in 2004 and 2005 reflects a true absence of a treatment effect in the study area. Power was poor in 2003 because of the low sample size and higher variability of the data; only imposed fishing effects of 50% or more would have given a high probability of correctly detecting a difference between treatment and control groups. In 2004 and 2005, however, full replication of the experiment resulted in good power. We were able to detect differences at 25–30% fishing effects in the 2004 experiment and at as low as 20% fishing effects in 2005.

We verified that substantial fishing removals occurred within the trawled portion of the study area during our experiment. The reported January–March fish harvest data from the NMFS Alaska Regional Office indicated that the harvest of Pacific cod by bottom trawl gear in the two federal reporting areas around Cape Sarichef was on the order of 25,000 metric tons (t) per year. Based on observed hauls, approximately 45% of the total harvest in these two reporting areas came from the study area (Table 2).

Table 2

Estimation of the Pacific cod (*Gadus macrocephalus*) harvest from the study area. Total Pacific cod catch during the winter trawl season in each year is shown for National Marine Fisheries Service reporting areas 509 and 517, which included the study area. Catch data from observed hauls were used to estimate the proportion of cod catch taken from a 1° latitude-longitude block around the study area; this proportion applied to the total harvest was used to show the approximate harvest (in metric tons) from the study area during the experiment.

	Estimated harvest (metric tons) taken with bottom trawl gear		
Year	Reporting areas	Study area	Proportion
2003	20,971	10,215	48.7%
2004	25,158	12,295	48.9%
2005	29,870	13,882	46.5%

Auxiliary biological and tagging data were useful for interpreting our results. Sex ratio and length–frequency data collected during each cruise indicated that the population of fish sampled sometimes changed substantially, even within the two-week duration of a study cruise. Sex and maturity class data from systematic subsamples of Pacific cod collected during the March 2004 cruise are shown in Figure 5. Although shifts from developing and prespawning stages to ripe and spent stages may reflect seasonal maturation of individual fish, differences in the proportion of mature to immature fish can only be explained by movement of fish into and out of the study area during the two-week period of the cruise. The overall sex ratio for the 15–22 March samples was 0.93 (males/female), whereas the sex ratio for 23–20 March was 0.75. This difference represents a significant change in sex ratio (P=0.0004) over the two-week period.

Qualitative tagging studies were conducted concurrently with the localized depletion experiment. Although these studies are to be reported separately, some of their results help to explain the outcome of the localized depletion experiment. Partial results from the February 2003 tagging studies indicated substantial movement of Pacific cod, both over spans of several months and over shorter time scales (Table 3). Over 70% of the fish released in the study area in February 2003 and recovered within two weeks of release were recaptured

more than 18.5 km (10 nmi, the radius of the notrawl zone) from their release location. The majority of fish recaptures took place east and slightly north of the release site within the Cape Sarichef notrawl zone, and only a few recaptures were documented for the study area immediately outside the notrawl zone.

Discussion

The results of our experiment were extremely clear. Although the direction and magnitude of the net seasonal change in abundance differed between study years, in each study year direction and magnitude of the percentage change (δ) were similar in the trawled and untrawled areas. Nonparametric tests used to compare δ's from the two zones consistently had *P*-values over 70%, indicating that there was no evidence that the distribution of the two groups differed—a conclusion that is evident without any statistical testing simply by comparing the frequency distributions of the δ's in the trawled and untrawled zones (Fig. 4). Analysis of the raw catch data with linear models leads to the same conclusion. Checks for more subtle indications of fishing effects, such as spatial patterns in catch within the study region or temporal trends within each two-week cruise, were also negative. These experimental results are inconsistent with the hypothesis of strong stationary localized depletion at the scale of the existing notrawl zones in Alaska.

Power simulations indicated that the failure to see a difference between trawled and untrawled areas was not simply due to a lack of resolution in the data. Although the sample size for 2003 was low, results for 2004 and 2005 showed that fishing removals that resulted in a 20–30% decline in catch rates in the trawled area would have been detected. There is little information on the size and duration of prey density decreases that would be necessary to impact Steller sea lion foraging success. It is possible that Pacific cod abundance in the study area was so high that even the substantial fishing removals resulted in a <20% change in local Pacific cod abundance. If this is the case, then the question becomes one of whether or not such small changes in prey availability would significantly affect Steller sea lion foraging.

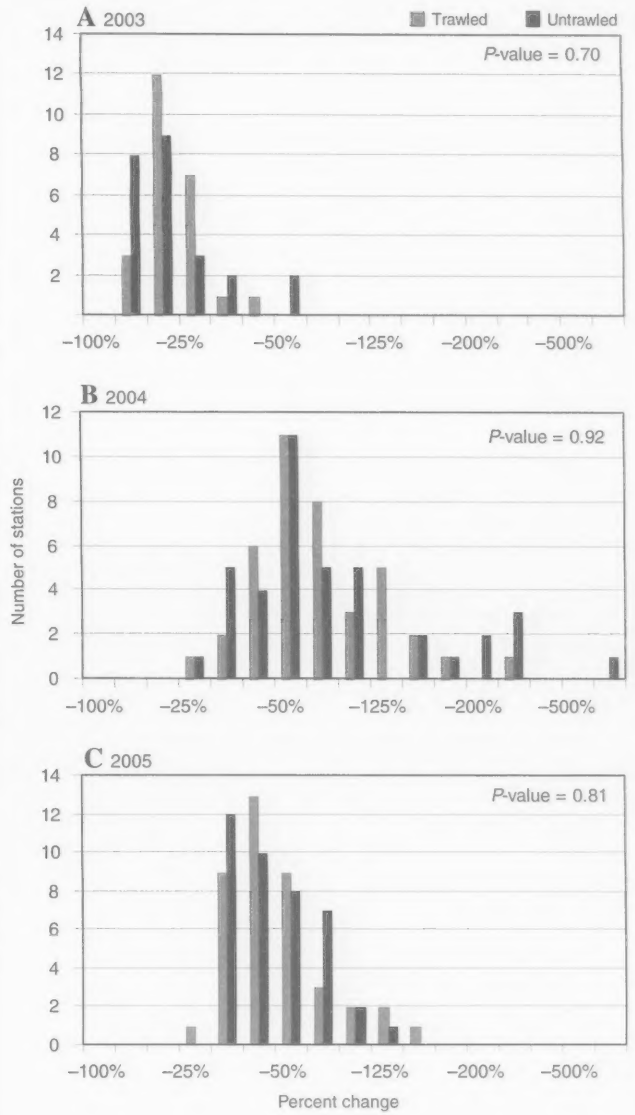

Figure 4

Frequency distribution of seasonal percent change in abundance (δ) for the Cape Sarichef localized depletion study. Dark bars are frequencies of δ for untrawled stations inside the notrawl zone, and hatched bars represent trawled stations outside the notrawl zone boundary: (**A**) 2003, (**B**) 2004, and (**C**) 2005. *P*-values for the nonparametric rank-sum test are shown in each figure.

Data from the auxiliary tagging and biological studies clearly indicated that Pacific cod in our study area were highly mobile over much shorter time scales than previously assumed. The stationary localized depletion scenario is based on the assumption of a closed local pool of fish that is reduced by local removals. Both the tagging data and the observed shifts in maturity and

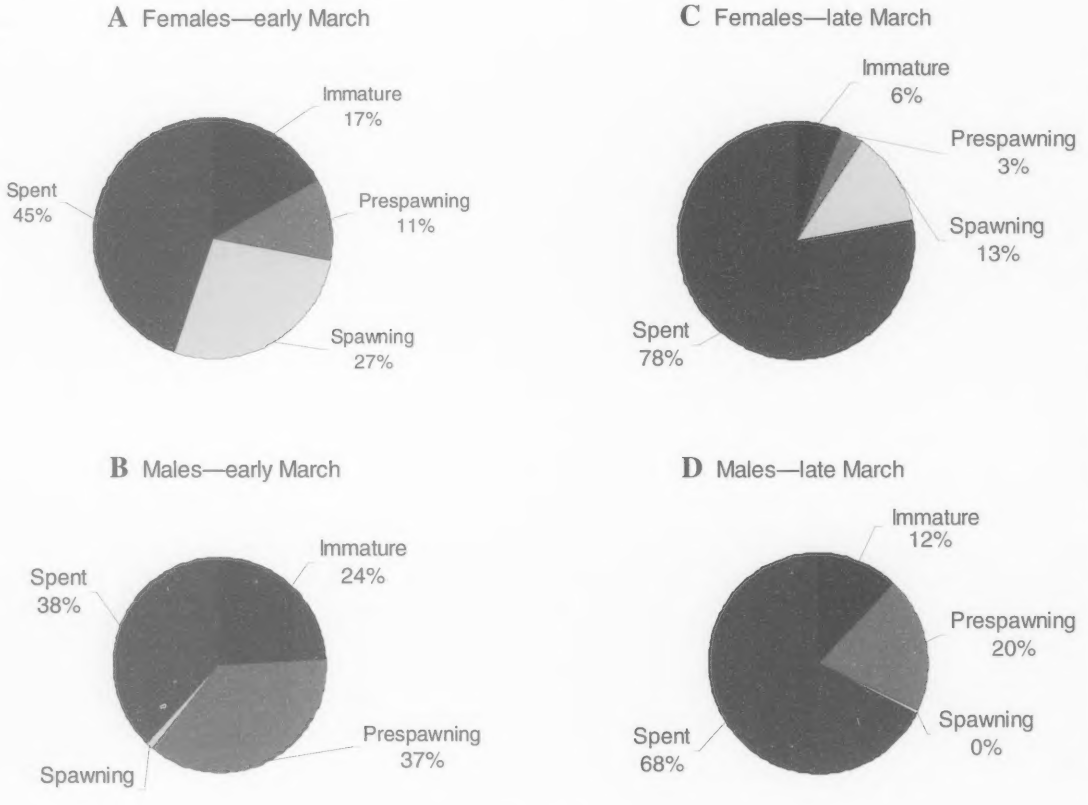

Figure 5

Gonad maturity stages for Pacific cod (*Gadus macrocephalus*) caught in March 2004. Fish were classified as immature, prespawning, spawning, or spent (immediately postspawning) based on visual inspection of the gonad. (**A**) females in randomly sampled catch from 15 through 22 March 2004, (**B**) males from this period, (**C**) females in randomly sampled catch from the same locations in 23–30 March 2004, and (**D**) males from this period.

sex ratio indicate that the local population of Pacific cod in our study area was not a closed, static pool of fish but a shifting, dynamic mix. In fact, the tagging data indicate that the short-term movement scale for Pacific cod in this region is substantially larger than the 10 nmi notrawl zone. Although fishing removal may have had an immediate localized effect on fish abundance, the effect was obscured by rapid fish movement (less than one week) over a geographic scale greater than that of the fishery removal. Thus, of the three localized depletion scenarios presented earlier (see *Introduction*), our results strongly disagree with conjecture one (stationary localized depletion). Because the experiment was limited in scale, our results do not eliminate the possibility of conjectures two and three (regional effects over larger spatial scales or displaced effects due to directed movement). Recent hydroacoustic studies of walleye pollock (*Theragra chalcogramma*) abundance in the same region (Barbeaux et al.[1]) also indicated attenuation of fishery-removal effects by rapid fish movement. Barbeaux et al. saw a visible pattern in echo sign during fishing, but diurnal fish movements eliminated the pattern within 12–24 hours.

The movement of Pacific cod, as qualitatively observed in the tagging data, could appear as a decline in catch rates for catch data measured on the same geographic scale. In a previous study of possible effects of commercial fishing on Pacific cod abundance (Fritz and Brown, 2005), commercial catch-per-unit-of-effort (CPUE) data were collected from a large region of the southeast Bering Sea, including our study area. Fritz and Brown interpreted a decreasing trend in fishery CPUE from

[1] Barbeaux, S. J., M. Dorn, J. Ianelli, and J. Horne. 2005. Visualizing Alaska pollock (*Theragra chalcogramma*) aggregation dynamics. ICES Council Meeting 2005/U:01.

Table 3

Partial results from tagged Pacific cod (*Gadus macrocephalus*) released near Cape Sarichef in February 2003, showing net movement of tagged fish. Table columns show distance travelled (km) between release and recapture points of a tagged fish. Table rows show weeks at liberty (the time elapsed between release and recapture dates). Table values show the percentage of recovered tags for which the distance travelled is within the specified range.

	Distance (km)						
Weeks at liberty	<9.3	9.3–18.5	18.5–37.0	37.0–74.1	74.1–148.2	>148.2	Number of tags recovered
<2	12.2%	15.1%	25.9%	18.0%	3.6%	25.2%	139
2–4	7.0%	2.3%	9.3%	34.9%	23.3%	23.3%	43
4–8	2.9%	5.9%	5.9%	26.5%	32.4%	26.5%	34
8–16	18.8%	12.5%	6.3%	25.0%	6.3%	31.3%	16

13 February through 24 March 2001 as localized depletion due to fishing removals. The models used in the Fritz and Brown study (the models of Leslie and Davis, 1939, and DeLury, 1947) are based on the assumptions of a closed population and constant catchability. These models are unable to distinguish between changes in abundance due to fishing removals and those due to fish dispersal or movement across the boundaries of the study area. If the assumption of a closed population is true, then declining CPUE would indicate a regional-scale effect (conjecture two). Given the high mobility indicated in Table 3, however, we doubt that the model assumptions are met for Pacific cod. Understanding patterns in Pacific cod abundance must take into account both substantial short-term movement and seasonal processes of migration and aggregation related to spawning.

The formal statistical inference presented in the present study applies only to the study area; extending this inference to other areas is reasonable but can only be considered a qualitative exercise. As with many comparative environmental studies, this project included only two experimental units, in the sense that the treatment (trawling) was applied to one region and the other region (notrawl zone) was used as a control. Hurlbert (1984) pointed out that, in an observational study with only one treatment and one control area, a statistical test constitutes evidence only for a difference between the two observed areas. The observation of an effect (or lack of effect) must be combined with biological knowledge of the system to extend inference from the observed areas to other parts of the system. In the case of Cape Sarichef, the experimental area was selected not as a representative location for the entire Bering Sea, but as the location where trawl fishing was most intensive and most likely to produce measurable local effects. Qualitative inference to other areas will require consideration of similarities in fishing pressure, Pacific cod behavior, and Pacific cod movement.

Localized depletion has not been widely discussed in the scientific literature. It has been proposed as a mechanism primarily in coral and sedentary benthic species (Gorfine et al., 2001; Jamieson, 2001; Harriott, 2003; Smith et al., 2004). Our results demonstrate that the mobility of the target organism must be considered in looking for localized spatial effects on groundfish. If localized depletion is to occur, it will result from the interaction of fishing pressure, fish abundance, and fish movement. To evaluate the impacts of fishery removals on other predators, such as Steller sea lions, the relevant scales of fishing, fish movement, and predator feeding must be clearly defined and understood. For Pacific cod, the very small spatial scale associated with the current regulatory notrawl zones appears to be smaller than the relevant scale of fish movement. Potential fishery effects at broader spatial and temporal scales may be more appropriately addressed by continuing to manage seasonal and spatial dispersal of the Pacific cod harvest.

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Comparison of echogram measurements against data expectations and assumptions for distinguishing seafloor substrates

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Abstract—Defining types of seafloor substrate and relating them to the distribution of fish and invertebrates is an important but difficult goal. An examination of the processing steps of a commercial acoustics analyzing software program, as well as the data values produced by the proprietary first echo measurements, revealed potential benefits and drawbacks for distinguishing acoustically distinct seafloor substrates. The positive aspects were convenient processing steps such as gain adjustment, accurate bottom picking, ease of bad data exclusion, and the ability to average across successive pings in order to increase the signal-to-noise ratio. A noteworthy drawback with the processing was the potential for accidental inclusion of a second echo as if it were part of the first echo. Detailed examination of the echogram measurements quantified the amount of collinearity, revealed the lack of standardization (subtraction of mean, division by standard deviation) before principal components analysis (PCA), and showed correlations of individual echogram measurements with depth and seafloor slope. Despite the facility of the software, these previously unknown processing pitfalls and echogram measurement characteristics may have created data artifacts that generated user-derived substrate classifications, rather than actual seafloor substrate types.

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Marine natural resource managers must define essential fish habitat (EFH) for federally managed, commercially exploited species (Federal Register, 2002) but the best method for fulfilling this mandate across the vast area and significant depths of the U.S. Exclusive Economic Zone remains unknown. A successful acoustic method for determining EFH would be of great benefit, because single-beam seafloor echosounder reflections are collected simultaneously with fish density estimates during National Marine Fisheries Service (NMFS) stock assessment bottom trawl surveys in the Gulf of Alaska (~800 stations among 320,000 km^2, ≤1000 m depth) and the Aleutian Islands (~400 stations among 67,000 km^2, ≤500 m depth). Therefore we conducted an acoustic analysis on data from a small portion from one survey in order to determine if there was a direct correlation between substrate classes or echogram measurements with species abundance.

We tested a widely used, proprietary software package (vers. 3.30, QTC IMPACT™), developed by the Quester Tangent Corporation (QTC, Sidney, British Columbia, Canada), to resolve the echosounder reflections into substrate types for comparison with the survey trawl catch data to determine whether there was a correlation or relationship between seafloor substrate classes and fish-density. This software produces 166 proprietary unitless echogram measurements (EMs) on the first seafloor echo for an internal principal components analysis (PCA), and then uses the first three principal components (PCs), generally accounting for more than 95% of the covariance (Ellingsen et al., 2002; Legendre et al., 2002) in *K*-means clustering, for dividing the first seafloor echoes into acoustically distinct substrate types.

Our initial efforts with *K*-means clustering indicated that a solution of any particular number of classes was not much better than other solutions (e.g., four versus five substrate classes), and therefore the 166 EMs were analyzed to determine if they could be used in another analysis for resolving substrate types. Although the general manner in which the 166 EMs, or the data, are acquired, processed, and divided into substrate classes by QTC software has been well reported in the literature, many specific details are lacking and it was therefore not clear what these 166 EMs represent.

To investigate an acoustic method for determining EFH we described the specific details of the processing method that QTC software follows, focusing on potential pitfalls and advantages for the user. We report on new findings based on some simple data explorations on the 166 EMs from echosounder data collected during a 2003 NMFS research cruise; and our findings are corroborated with four data sets collected independently from other agencies on other ships. In this analysis we checked the assumption that these 166 EMs have the same scale or range as that normally used in PCA, and the as-

Table 1

Details of echosounder research cruises and of the data collected from these cruises from 1999–2004 for a study to determine whether there is a correlation between echogram measurements and species abundance. Codes for agencies: NMFS, National Marine Fisheries Service; ADFG, Alaska Department of Fish and Game; NIWA, New Zealand National Institute of Water and Atmosphere; DFO, Canadian Department of Fisheries and Oceans. QTC VIEW and QTC IMPACT are software products from QTC (Quester Tangent Corporation), Sidney, British Columbia, Canada. Reference depth is the depth for which depth-related changes in echo signal protraction were corrected. Stacks are groups of five echoes or acoustic returns that were summed together for analysis. Fully collinear echogram measurements were the number of values out of a possible 166 that caused the variance-covariance matrix determinant in a principal components analysis to be zero.

Vessel	Year	Location	Agency	Echo sounder	kHz	Sampling (Hz)	QTC VIEW vers.	QTC IMPACT vers.	Reference depth (m)	Depth range (m)	Stacks	Number of fully collinear echogram measurements
FV *Gladiator*	2003	Gulf of Alaska	NMFS	Simrad	38	977	none	3.30	50	25–100	14,432	155
FV *Gladiator*	2003	Gulf of Alaska	NMFS	Simrad	38	977	none	3.30	150	100–200	3598	155
RV *Resolution*	2003	Gulf of Alaska	ADFG	Biosonics 101	120	20,000	3.25	3.3	100	66–136	3680	152
RV *Rangithi*	1999	New Zealand	NIWA	Simrad EA501P	200	20,000	4	2	10	4–15	736	148
RV *Pallasi*	2004	B.C., Canada	DFO	Furuno	50	20,000	4	3.4	12	3–34	736	155
RV *John P. Tully*	2002	B.C., Canada	DFO	Simrad	50	20,828	5	3.20	50	64–132	727	152

sumption that these 166 EMs are derived from the first echo only. Because both of these assumptions are typically presumed to be correct for this type of acoustic analysis, these findings may be of use for interpreting seafloor substrate classifications for determining EFH.

Materials and methods

Data collection and conversion

Data were collected in the *.raw format from a 38-kHz Simrad single-beam echosounder on the FV *Gladiator* during the 2003 NMFS bottom trawl survey in the Gulf of Alaska (Table 1). The transducer gain was 24.5 dB, transmit power was 1500 W, beam angle was 9°, pulse length was 4.096 ms, and the sampling interval was 1.024 ms. These Simrad files were calibrated in EchoView® (vers. 3.30.60.05, SonarData Pty. Ltd, Hobart, Tasmania, Australia), and short (~1.5 km, ~1440 pings) seafloor sections corresponding to 15-minute duration bottom tows conducted at 1.54 m/s (3 knots) were exported into binary files by using the EchoImpact export module for import into QTC IMPACT™. This EchoImpact export module was specifically designed by the two companies to convey acoustic data in an appropriate format from EchoView to QTC IMPACT. We also examined EMs recorded directly by QTC VIEW™ (QTC, Sidney, British Columbia, Canada), without any prior EchoView® processing, at preset gains (ping intensities or amplitudes) by four external research cruises: the Alaska Department of Fish and Game (ADFG RV *Resolution* 2003 cruise), the Canadian Department of Fisheries and Oceans (Canadian coast guard ship RV *John P. Tully* 2002 cruise, and the RV *Pallasi* 2004 cruise), and the New Zealand National Institute of Water and Atmosphere (RV *Rangithi* 1999 cruise) (Table 1).

Gain settings

In automated seafloor echo-processing systems, there may be a mismatch between the seafloor echo strength (gain) and the ability of the processing system to identify the abrupt rise or spike that represents the beginning of the seafloor reflection. It is necessary to adjust the gain setting such that the inflection point can be distinguished from the earlier portion of the echo, which is the water column above the seafloor. Therefore several postprocessing gain settings in QTC IMPACT were applied to subsets of the NMFS 2003 FV *Gladiator* data sets in order to maximize the number of pings strong enough for automatic bottom detection (or bottom picking) and to minimize the number of pings that would be too strong for the dynamic range of 96 dB of sound that QTC software can process. Otherwise, louder portions of pings would have had to have been automatically decreased to 0 dB, a process known as clipping, and quieter portions of pings would have had to be automati-

cally increased to –96 dB. Another convenience of the QTC software was that abnormally weak echoes could be eliminated by specifying a minimal signal strength, and this was set to be equal to 25% of the maximum permissible amount (0 dB).

Bottom picks

After importing the recorded echoes into the software at an appropriate gain setting, another method for further improving the signal-to-noise ratio would be to assemble a stack of successive echoes, presumably from the same substrate, and average the echo stack into a single echo (Pace and Ceen, 1982). For QTC IMPACT, a minimum stack size of five pings was recommended, which corresponded to 2.5 seconds or 3.85 m traveled at 1.54 m/s, for a theoretical yield of 288 stacks per trawl path. The strong, positive benefits of stacking were dependent on correctly aligning events with the successive echoes, and therefore on the software's interpretation of the seafloor inflection point. Although this data check is not mentioned in the literature, it is a critical part of the process, because all measurements start at the seafloor inflection point. We examined every bottom pick for appropriate placement, as recommended by QTC guidelines. This process determined that the bottom pick was not interpolated between sample intervals, and that the natural variability of the depth among a group of pings would be the distance sound travels during half the sampling interval (0.768 m).

Generating echogram measurements

Once the bottom pick had been located, an automatic determination of the length or extent of any seafloor echo was difficult because rough, steep, soft, and deep areas have longer reflections than smooth, flat, hard, and shallow areas. The QTC IMPACT software uses 256 sound samples of vertical time intervals, or recorded sound intensity within a ping, surrounding the bottom pick. Starting at the bottom pick, five samples (representing the water column) were taken above the seafloor inflection point and 251 samples were taken below the start of the first seafloor reflection (representing the seafloor). If the echograms contained fewer than 251 time intervals below the start of the first seafloor reflection, the last sample was repeated (padded) as many times as needed until the 251 sample requirement was fulfilled. The QTC software then generated 166 EMs for each stack with reference to a specific depth such that depth-related changes in signal protraction were corrected.

Optimum substrate classification

Organizing the echogram measurements along a continuum of measurements or grouping them into a number of acoustically distinct substrate classes is the final step in the process. Ideally this step would identify substrate qualities of importance to EFH species, such that researchers could infer essential fish habitat from substrate types and use this information for better resource management. The QTC method first uses continua by performing PCA on the 166 EMs and retaining the first three PCs for plotting the location of each stack in three-dimensional space. Then it is up to the user to determine the optimum number of substrate classes on the basis of the *K*-means clustering of the first three PCs.

Examination of the data

Because the algorithms for producing the 166 EMs are proprietary, the data values produced by the 166 EMs were exported and viewed in a text editor, which showed that the data values for each stack were displayed as seven decimal-place numbers in four columns, underneath a stack header. In order to resolve the possible complications of having a single set of 166 EMs for five different stacked pings, a single ping was exported from EchoView® and imported into QTC IMPACT five times, to create one stack of identical pings. The four columns of 166 EMs were reformatted into a single column in a spreadsheet and an examination of the data revealed that the EMs from this single, repeated ping were occurring in five groups (von Szalay, 1998).

Variability and covariance of echogram measurements

Simple data checks, such as checks of averages, variances, minima, and maxima, enabled us to describe each data set and determine the range or scale of each EM. The variance between EMs, or the covariance, was derived to determine the amount of collinearity among the EMs.

Correlation of echogram measurements with depth

The correlation between each EM versus depth was determined from each of the data sets. This simple analysis, which could provide some useful diagnostics, has not been reported in any of the literature.

Angle of incidence

The angle of echosounder seafloor reflections has a potentially confounding influence on any depth-correlation analysis, because the rate of change of depth and slope vary together. In general, QTC and similar products should be used to analyze normal (90°) incident reflections (see Pace and Ceen, 1982; Orlowski, 1984), and it is expected that severe departures from normality would cause analytical failures. The influence of non-normal (<90°) reflections could not be formally examined in our study because of a lack of knowledge about cross-track slope, vessel pitch and roll, and interactions between seafloor angle and vessel angle. However, more single-beam data were analyzed from the FV *Gladiator* in 2005 at small study sites in the Aleutian Islands that had been groundtruthed with video and multibeam sonar equipment in 2004, such that the substrate types

and seafloor slopes were known (Rooper and Zimmermann, 2007).

Assumption 1: scale of measurements

Although as a group the 166 EMs ranged between zero and one (Legendre et al., 2002), this was tested for each of the 166 EMs; and EMs fully extending across this range would indicate that the data had been standardized for proper PCA (Manly, 1994; Legendre and Legendre, 1998). PCA was also conducted (S-Plus, vers. 6.1, Insightful Corp., Seattle, WA) independently to ensure that the QTC PCA results could be reproduced.

Assumption two: first echo

Although it is widely reported or implied in the literature that QTC IMPACT software analyzes only the first echo, that conclusion is not strictly correct. QTC IMPACT analyzes the first 251 sound samples beneath the bottom pick, and it is up to the user to ensure that this is a meaningful window. The relationship between the 251 samples and the analysis depth range is directly related to half of the sample interval preset in the echosounder;

$$\textit{Analysis depth range}\ (\text{m}) = \textit{Sample interval}\ (\text{s/sample}) \times (0.5) \times (1500\ \text{m/s}) \times 251\ \text{samples},$$

where 1500 m/s = the approximate speed of sound through seawater.

This relationship was tested to determine how well the 251 sample size corresponded with the first echo in the NMFS 2003 FV *Gladiator* data sets and with the external data sets collected by other agencies from other vessels.

Results

Gain settings

Determining the proper gain setting for the NMFS 2003 FV *Gladiator* data sets was a time-intensive process because a wide range of gains needed to be applied and weak or bad data had not yet been identified. We determined that a gain setting of –18 dB would be appropriate for shallow sites (25–100 m, 68 sites, 97,119 pings) and a gain setting of –17 dB would be appropriate for deep trawl sites (100–200 m, 19 sites, 25,110 pings). Several additional sites with too many weak pings (>50%), an indication of bad data, were identified and eliminated from processing at this stage. Although changing the gain setting within QTC IMPACT by 0.5 dB was equivalent to changing the gain setting by 1.0 dB in EchoView®, use of the gain adjustment within QTC IMPACT was far more convenient for adjusting the echo signal strength to be within the required 96-dB range, and for identifying bad data.

Bottom picks

In the NMFS 2003 FV *Gladiator* data sets, there were 72,296 shallow (25–100 m) pings with bottom picks including 3961 that were clipped, and there were 18,021 deep (100–200 m) pings with bottom picks including 1106 of those that were clipped. Thus there was a greater than 70% success rate in bottom picking and approximately 6% clipping among both data sets, indicating that the gain settings were appropriate. Each bottom pick was inspected and found to occur anywhere between the base and the tip of the peak—in the general region of the seafloor location. Thus QTC IMPACT software did an excellent job of bottom picking in the NMFS 2003 FV *Gladiator* shallow and deep data sets.

Generating echogram measurements

The NMFS 2003 FV *Gladiator* shallow data set yielded 14,432 stacks (of five pings) and the deep data set yielded 3598 stacks (of five pings); odd lots of fewer than five pings were not included in stacks, and therefore the total number of stacks was slightly less than one fifth of the total number of pings with bottom picks. Padding was required at all shallow sites for all of the stacks, and padding was required at 16 of 19 deep sites on a total of 3112 stacks. A reference depth of 50 m was used for the shallow sites and 150 m was used for the deep sites. The EMs for the shallow sites were combined into a single data set for PCA and *K*-means clustering. The process was repeated for the EMs from the deep sites.

Optimum substrate classification

The *K*-means clustering of the first three PCs indicated that a solution of any specific number of acoustically derived substrate classes would not explain much more of the variance than other solutions. Therefore the data processing was repeated several times to check for errors that may have influenced the results. The main focus was on gaining a better understanding of the numbers that were being created and processed with PCA and *K*-means clustering, and on exploring factors that may have affected the EMs.

Examination of the data

Examinations of the spreadsheets of EMs from the NMFS 2003 FV *Gladiator* shallow and deep data sets, and the four externally collected data sets, showed the same groups as those revealed by the examination of the stack of the single pings repeated five times; EMs 1–23, EMs 24–39, EMs 40–70, EMs 71–101, and EMs 102–166. Across all data sets, the EMs in the first (EMs 1–23) and fifth (EMs 102–166) groups were, in general, highly correlated with their neighbors (e.g., EM 22 versus 23, Fig. 1). In the second group of EMs (EMs 24–39), EM 31 was the sum of EM 32 through EM 39, each of which were fractions of 256 (e.g., 1/256, 2/256). Among the 31

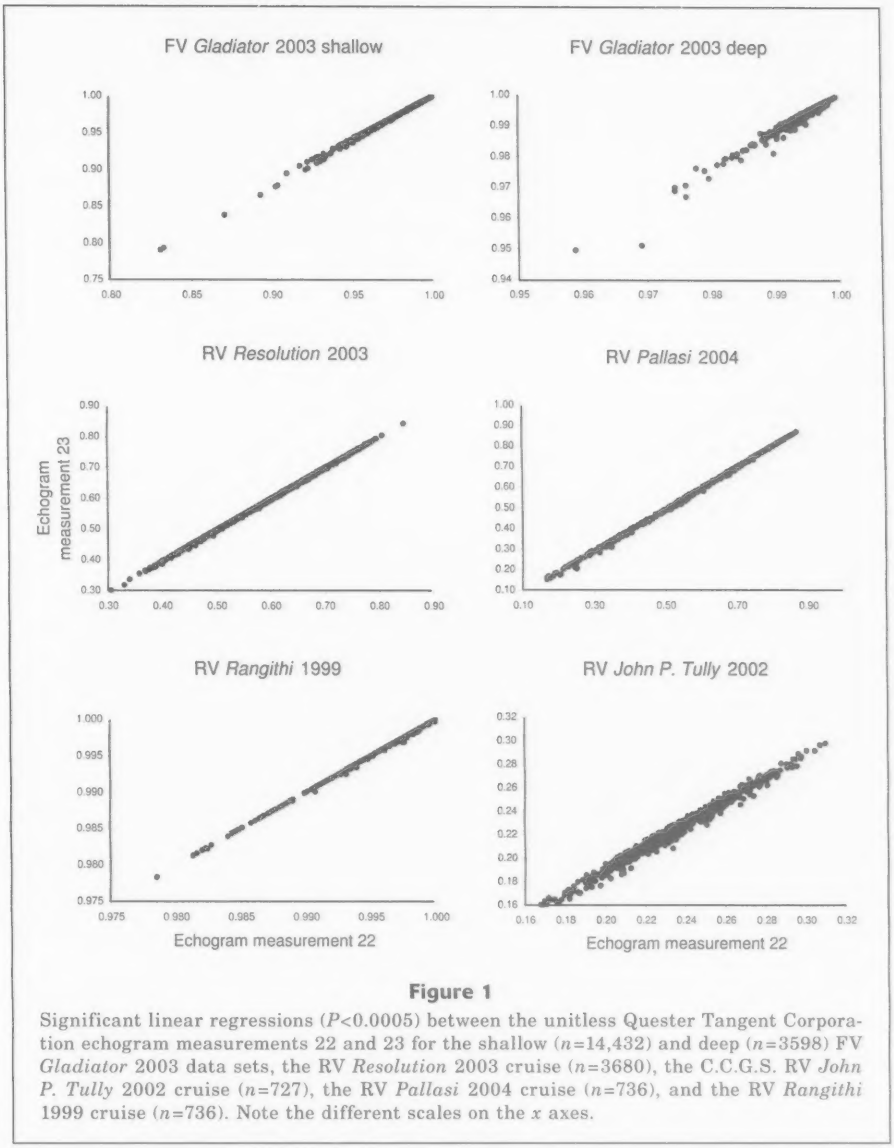

Figure 1

Significant linear regressions ($P<0.0005$) between the unitless Quester Tangent Corporation echogram measurements 22 and 23 for the shallow ($n=14,432$) and deep ($n=3598$) FV *Gladiator* 2003 data sets, the RV *Resolution* 2003 cruise ($n=3680$), the C.C.G.S. RV *John P. Tully* 2002 cruise ($n=727$), the RV *Pallasi* 2004 cruise ($n=736$), and the RV *Rangithi* 1999 cruise ($n=736$). Note the different scales on the x axes.

EMs in each of the third (EMs 40–70) and fourth (EMs 71–101) groups, there were 16 original EMs grouped into 15 succeeding sums, with the final EM (EM 40 in the third group and EM 71 in the fourth group) being the sum of the whole group (Fig. 2). In the third group, EM 40, which was always 1.0, was created by the sum of EM 41 and EM 56, which are complements to each other and therefore are entirely dependent.

Variability and covariance of echogram measurements

There were several unusual observations of variance or covariance among the 166 QTC IMPACT-generated EMs. Three EMs—16, 31, and 40—never varied (were always 1.0000000 or 0.9999999) and it is presumed these are the same three that Legendre et al. (2002) stated never varied from one. Additionally, three EMs from the RV *Rangithi* 1999 cruise data were always zero. Although it is difficult to describe all the dependent relationships (the sums and correlations) between the remaining 160 to 163 EMs, it is much simpler to note that among the six data sets, a range of 148 to 155 EMs (Table 1) were fully collinear (causing the variance-covariance matrix determinant to be zero; Neter et al., 1990). Among the eight to 12 EMs within each data set that were not fully collinear, four to

Initial sums	Secondary sums	Tertiary sums	Final sum
70 + 69 = 68			
67 + 66 = 65			
	68 + 65 = 64		
63 + 62 = 61			
60 + 59 = 58			
	61 + 58 = 57		
		64 + 57 = 56	
55 + 54 = 53			
52 + 51 = 50			
	53 + 50 = 49		
48 + 47 = 46			
45 + 44 = 43			
	46 + 43 = 42		
		49 + 42 = 41	
			56 + 41 = 40 = 1.000000

Figure 2

Schematic diagram depicting a sequence (from left to right) of 15 sums from 16 original unitless echogram measurements—a sequence of sums that leads to a final sum of one. The left column shows how 16 original echogram measurements are summed into eight new echogram measurements. The next column shows how these eight sums are summed into four new echogram measurements. The third column shows how these four sums are summed into two new echogram measurements. The fourth column shows how these two sums are summed to produce a final echogram measurement of one.

seven EMs had variance inflation factors >10 (a general threshold indicating high correlations but not full collinearity with the remaining variables; Neter et al., 1990), leaving only three to six relatively independent EMs in each data set.

Correlation of echogram measurements with depth

There was a significant relationship between depth and some EMs in all data sets (Fig. 3). This relationship translated into significant relationships (LOESS curve fits) between PC1 and PC2 versus depth for all six data sets (F-tests, $P<0.001$), indicating that depth has a direct influence on the QTC substrate classification.

Angle of incidence

At the Aleutian Islands groundtruth site (FV *Gladiator* in 2005; Rooper and Zimmermann, 2007), there were significant linear correlations ($P<0.05$) between slope and EMs for the most common substrate classes of sand-boulder ($n=368$ video observations), sand-sand ($n=351$), and bedrock-boulder ($n=259$), even when the analyses were restricted to low (<5°) slopes (von Szalay, 1998; von Szalay and McConnaughey, 2002). The influence of slope resulted in EMs that were equivalent among different substrates and different slopes. For example, EM 1 on a substrate of bedrock-boulder at 1° slope was equivalent to EM 1 on sand-sand substrate at 4.1° slope, and equivalent to EM 1 on sand-boulder substrate at 4.9° slope (Fig. 4), illustrating how easily substrates can be misclassified at low slopes.

Assumption one: scale of measurements

The S-Plus version of PCA, conducted after eliminating invariant EMs (16, 31, and 40), confirmed that the QTC IMPACT method of PCA does not use any additional data ranging or standardization. PCA performed in S-Plus with standardization (subtraction of mean,

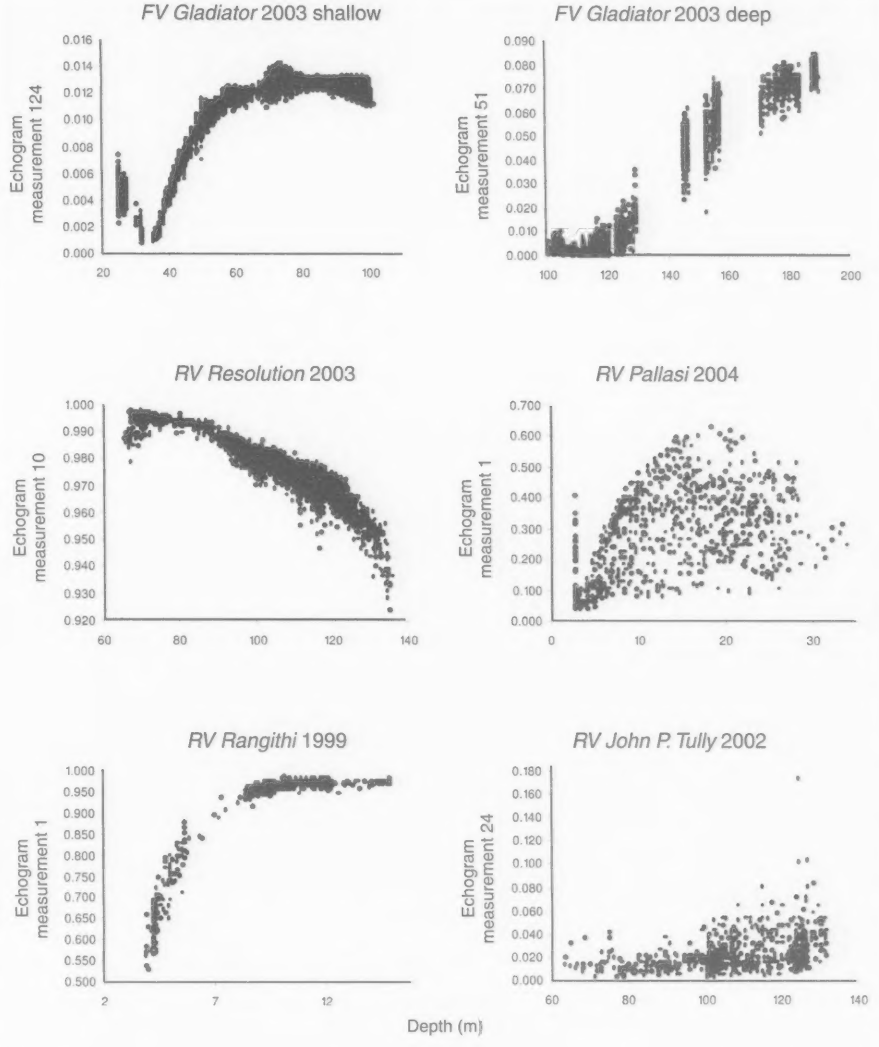

Figure 3

Significant relationships between QTC (Quester Tangent Corporation, Sidney, British Columbia, Canada) IMPACT™ generated echogram measurements and depth for the shallow and deep FV *Gladiator* 2003 data sets, the RV *Resolution* 2003 cruise, the C.C.G.S. RV *John P. Tully* 2002 cruise, the RV *Pallasi* 2004 cruise, and the RV *Rangithi* 1999 cruise. Note the different scales on the *x* axes.

division by standard deviation; Manly, 1994; Legendre and Legendre, 1998) revealed that more PCs were required to explain the same total amount of variance as the QTC IMPACT PCA method (Fig. 5). Thus the lack of standardization within the QTC IMPACT PCA method can have a strong effect. For example, across all six data sets, some EMs such as EM 15 were always large (≥0.938), some such as EM 166 were always small (≤0.006), and some such as EMs 1 and 102 generally had larger ranges and were more variable. Within the first group of EMs (1–23), EM 1 was always ≤ EM 2, EM 2 was always ≤ EM 3, etc., up to EM 16, which was always ≥ EM 17, which was always ≥ EM 18, etc., up to EM 23. Thus these variables have constricted ranges which can affect PCA. Additionally, the strong correlations between neighboring variables within the first (EMs 1–23) and fifth (EMs 102–166) groups indicate that these EMs are either measuring nearly the same echo component,

or that EMs are based on neighboring EMs. Without standardization of these correlated EMs, the amount of variance explained by the first three PCs is artificially inflated. The inclusion of sums of variables in a PCA, such as the 15 sums of variables in the third (EMs 40–70) and fourth (EMs 71–101) groups, also artificially inflates the amount of variance explained in a PCA. Inclusion of a variable that is a complement of another variable (EM 41 or EM 56) in a PCA does not improve or impair the results and one of these complements could be excluded, along with the three invariant variables.

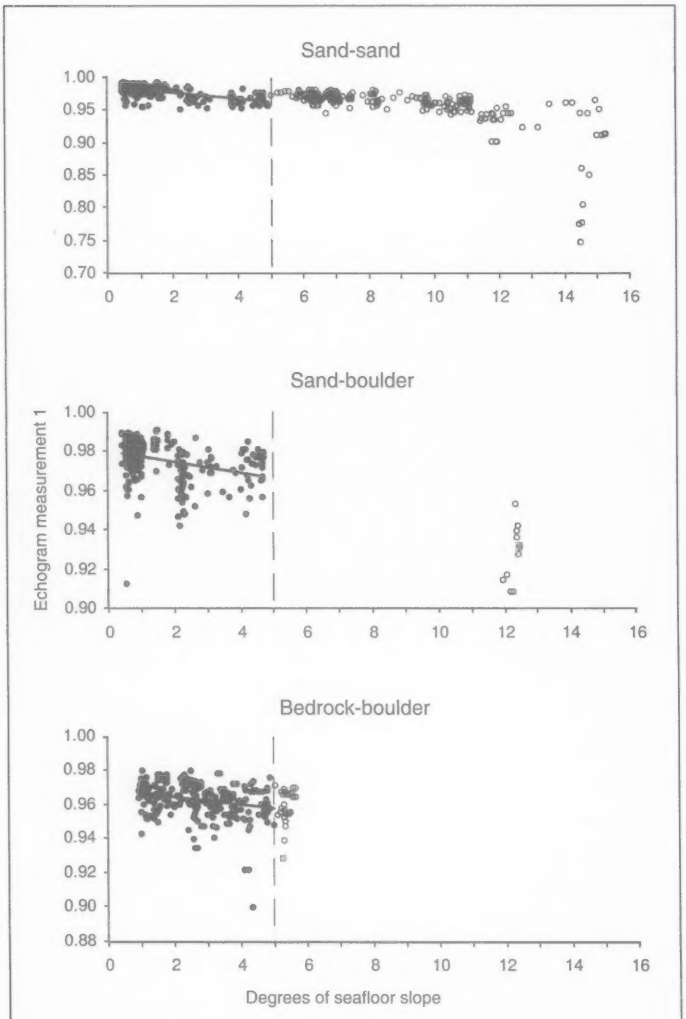

Figure 4

Significant linear regressions ($P<0.05$) between low seafloor slopes <5° (●) and QTC (Quester Tangent Corporation, Sidney, British Columbia, Canada) IMPACT™ echogram measurement 1, with observations from greater slopes (○) excluded from the regression analysis, for the three most common substrate types found during the FV *Gladiator* 2005 cruise. Only data values to the left of the 5° mark (dashed vertical line) were included in the regression analysis.

Assumption two: first echo

The 251 sampling envelope used with the QTC IMPACT software may be a mismatch for the actual length of the first echo. In the FV *Gladiator* 2003 shallow and deep data sets (both <200 m), the 251 sampling intervals of 977 Hz or 0.001024 s translated into an excessive and unnecessary 192.8 m analysis depth range below the start of the first seafloor reflection, a fact not realized during the collection of the echosounder data. However, the recording of most of the *.raw files were truncated before the full 192.8 m distance, before any second echo, and also before the full 251 samples; therefore most of the echoes needed padding (extended repetition of the last sound sample in the echo). The second echo was recorded in the *.raw file and it fell within the ≤51 sample requirement in 19 of the 68 shallow sites (25–100 m) and four of the 19 deep sites (100–200 m). These same pings were exported from EchoView® to QTC IMPACT with and without the second echo, and our analyses demonstrated that QTC IMPACT treated the second echo as if it were part of the first echo. The accidental inclusion of the seafloor spike from this second echo reduced the values of the first 23 EMs (except EM 16) and had the greatest effect when the seafloor spike of the second echo occurred at the edge of the export window, where it was repeated to fulfill the 251 sample requirement (see Haul 206, Fig. 6). There was less of an effect when more of the second seafloor spike was included, so that the padded value was of lower sound intensity (see Haul 124, Fig. 6). Thus significant differences in some of the echogram measurements can be created for the exact same substrate type if users are not careful about ensuring that the 251 sample window of QTC IMPACT matches up well with the first echo length.

Discussion

Although this analysis demonstrated that there are several strong advantages (gain adjustment, bottom picking, bad data exclusion, and stacking) in using the partially automated echogram classifying software (QTC IMPACT), there are also several potential pitfalls (dependencies among the 166 EMs, lack of standardization, correlation with depth, influence of seafloor slope, and mismatch between 251 sample

intervals versus first echo length), such that it does not function as users would expect for distinguishing substrate types. There are also several processing steps within QTC IMPACT, such as repeating the last sample of short pings (padding), reducing the strength of sections of pings that are too strong, and increasing the strength of sections of pings that are too weak, all of which may affect analyses. The proprietary nature of the software and the internal processing steps have discouraged user criticism and examination of the QTC IMPACT generated data (Kloser et al., 2001). QTC IMPACT users should export, format, and carefully examine their 166 EMs before substrate classification in order to catch user-generated mistakes, such as accidentally including a second echo, and to identify and remove any constant or collinear EMs. After analysis of the EMs, users may be able to reduce the 166 EMs to fewer than 10 without any loss of information, and compare these against depth, slope, and substrate types, if known, for further data-checking. The first assumption—that the scale or range of the data were appropriate for PCA—was disproved, and users may want to consider whether standardizing is appropriate for their data. The second assumption—that QTC IMPACT only uses the first echo—is not necessarily true and published QTC IMPACT substrate classes may have been differentiated by the presence or absence of all or part of the second echo.

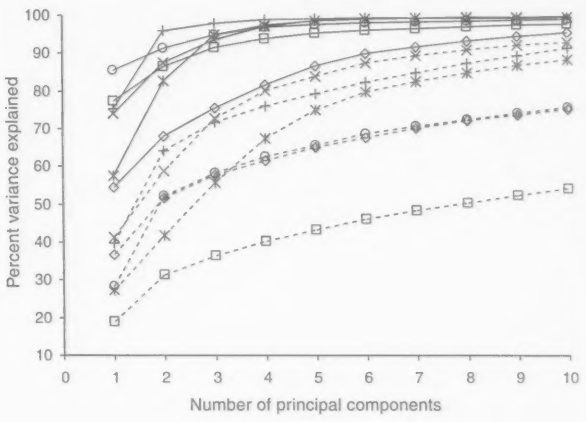

Figure 5

Percent of variance explained in principal components analysis (PCA) conducted on the echogram measurements produced by QTC (Quester Tangent Corporation, Sidney, British Columbia, Canada) IMPACT™ software when the data were not standardized (QTC method ——) and when the data were standardized (textbook method - - - -) for the RV *Resolution* 2003 cruise (□), the C.C.G.S. RV *John P. Tully* 2002 cruise (◇), the RV *Pallasi* 2004 cruise (○), the RV *Rangithi* 1999 cruise (+), and the NMFS FV *Gladiator* 2003 shallow (×) and deep (✳) cruises.

Optimum substrate classification

The inability to determine an optimum number of substrate classes for the shallow and deep FV *Gladiator* 2003 data sets is a common problem in seafloor substrate analysis and is not a critique of the particular *K*-means method within QTC IMPACT software. Our echosounder data could have been too noisy, too coarse, too affected by sea-state or seafloor slope, or our trawl sites could have been too variable or too constant for determining substrate classes. Instead, our results, with corroborations from independent data sets, indicated the importance of analyzing the echogram measurements before any PCA and *K*-means analysis so that depth-related and slope-related errors, second echo or echo envelope errors, and variable range or collinearity errors could be caught. The pros and cons of the QTC IMPACT method of *K*-means partitioning have already been thoroughly discussed. It was criticized by Legendre et al. (2002) who offered a new *K*-means method based on Euclidean distance. Preston and Kirlin (2003) responded by defending and elaborating on their *K*-means clustering method, which is based on Mahalanobis distance, and citing successful QTC IMPACT substrate-typing projects (Anderson, 2001; Morrison et al., 2001; Anderson et al., 2002; Ellingsen et al., 2002). Legendre (2003) offered additional criticism of the QTC IMPACT *K*-means clustering method and added that the QTC IMPACT method of clustering, based on only the first three principal components (PCs), was strongly influenced by depth, since his PC1 was strongly related to depth, as opposed to a solution that would include a greater number of PCs. Clearly the *K*-means method for distinguishing substrate classes is important, and strongly linked to the data values that feed into it.

Examination of the data and the variability and covariance of echogram measurements

This exploration of the 166 EMs provides the first description of the QTC IMPACT data set that is used for seafloor substrate classification. Before this description, only three EMs were known to be invariant and the rest were highly collinear (Legendre et al., 2002). These EMs were known to carried limited information and were highly redundant (Ellingsen et al., 2002). Researchers collecting data directly into QTC VIEW, such as corroborating data from different agencies, did not have the additional processing step of importing the data from EchoView®, and were probably unaware of the 96 dB dynamic range required for QTC IMPACT software. Therefore the effect of clipping portions of pings that were too loud, increasing the sound level of ping portions that were too quiet, or adding or subtracting a constant amount of sound to entire ping data sets (gain adjustment), was not widely reported in the literature. Only Anderson et al. (2002) mentioned experimenting with

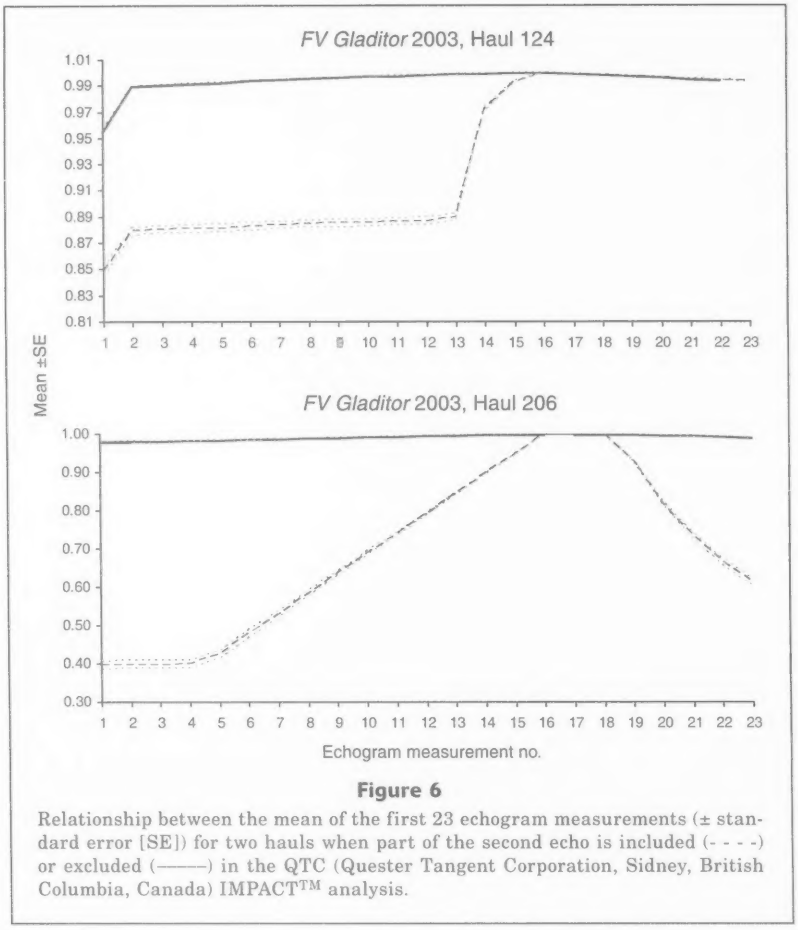

Figure 6

Relationship between the mean of the first 23 echogram measurements (± standard error [SE]) for two hauls when part of the second echo is included (- - - -) or excluded (———) in the QTC (Quester Tangent Corporation, Sidney, British Columbia, Canada) IMPACT™ analysis.

different gain settings and different reference depths. Users have also been unaware of the 251 sample requirement, or the effects of repeating the last sound sample (padding) in order to fulfill this requirement. Ellingsen et al. (2002) mentioned that truncated acoustic reflections resulted in a loss of some of the 166 EMs. Perhaps results from their field work resulted in modification to the QTC IMPACT software so that the last acoustic sample was repeated (a process known as padding).

Correlation of echogram measurements with depth

The influence of depth on the EMs, and on the resulting PCs, may be due to improper echosounder calibration or improper depth-correction in QTC IMPACT, rather than to true variation in substrate types. It is not possible for users to determine the origin of the depth influence. Although the reference depth is supposed to compensate for the signal-protraction of pings of different depths within a data set, none of the QTC IMPACT studies in the literature have actually checked to determine if such compensation occurs. It has been reported in the literature that the QTC IMPACT-generated PC1 is correlated with depth (Legendre, 2003) and that QTC IMPACT-generated substrate classes are sometimes correlated with depth (Anderson et al., 2002). As with our findings, depth biases were also reported for the E1 (roughness) and E2 (hardness) measurements made by RoxAnn™ (Sonavision, Aberdeen, Scotland, U.K.) bottom-typing software, as determined by a more thorough study with careful seafloor groundtruthing (Kloser et al., 2001).

Angle of incidence

Any potential effect due to impact angle of echogram reflection, which is a combination of seafloor slope and vessel motion, is not widely addressed in the literature. Anderson (2001) used QTC VIEW™ to distinguish among substrates on steep slopes, some of which appear to be as steep as 45° (see Anderson, 2001, Figs. 4 and 5), whereas von Szalay (1998) and von Szalay and McConnaughey (2002) reported that

seafloor slopes exceeding 5° to 8° caused significant substrate misclassification. In Ellingsen et al. (2002), effects from vessel motion may have been reduced or eliminated by working in calm seas. Our analysis of individual EMs revealed the mechanism whereby substrates may be misclassified in areas with slope and we would suggest that there is greater sensitivity with QTC VIEW than previously noted by von Szalay (1998) and von Szalay and McConnaughey (2002). The QTC IMPACT method of stacking multiple pings could potentially ameliorate the influence of slope-affected pings, but it could also create new substrate classes by combining normal and non-normal reflections. Although it is presumed that QTC IMPACT software could distinguish among substrates at a constant depth in a flat seafloor area with no vessel pitch and roll, this type of situation is not realistic for the NMFS bottom trawl surveys in the Gulf of Alaska and Aleutians Islands. If steep seafloor areas can be distinguished from vessel motion through careful incorporation of vessel motion measurements, slope may be considered as a substrate modifier or as a significantly different substrate, depending on the species of interest for which habitat is being defined.

Assumption one: scale of measurements

The QTC IMPACT method of PCA (without standardization of data) results in a higher amount of variance explained because it is based on a few variables with the highest variance, which are also highly correlated. Those EMs without much variance only make a minor contribution to the PCA solution; however, it remains unclear whether forcing EMs to vary through standardization—a process that could possibly include both discriminating (signal) and nondiscriminating measures (noise) of echo energy, timespread, and skewness (van Walree et al., 2005)—increases or decreases statistical power for discriminating substrate types. The user is left having to choose between conducting a nonstandardized PCA where nearly all variables are collinear or conducting a standardized PCA that may be based mostly on noise. Including fully collinear (e.g., the sums of) variables and correlated variables in a PCA does not provide additional discriminatory information, but it does change the results. Therefore users may find it beneficial to conduct an additional PCA without these collinear variables and determine how much the substrate groupings change. Perhaps not coincidentally, our findings that only three to six variables within each of the acoustic data sets were somewhat independent (provided discriminatory power) matches well with van Walree et al.'s (2005) description of six acoustic algorithms and Kloser et al.'s (2001) description of four algorithms. Our results indicate that the EMs are not standardized before PCA, and because this is not mentioned in the literature, it may be an unexpected problem for users. The lack of standardization among collinear and correlated variables might partly explain why QTC IMPACT software typically requires only three eigenvectors to explain more than 95% of covariance (Ellingsen et al., 2002; Legendre et al., 2002).

Assumption two: first echo

Surveys conducted in shallow water with high sampling rates and surveys conducted in deep water with low sampling rates (such as that of the NMFS 2003 FV *Gladiator*) are equally vulnerable to accidentally including second, or later, seafloor reflections in QTC IMPACT analysis. For example, the RV *Rangithi* 1999 and RV *Pallasi* 2004 data sets both required 9.4 m below the start of the first seafloor reflection to achieve 251 samples, but the range of these data sets was shallower (Table 1). Because both of these data sets were recorded directly into QTC VIEW, the raw data could not be examined to determine if additional echoes were recorded or not. However, both data sets had characteristic drops in the values of the first group of EMs between approximately 9 and 4 m depth, indicating a probable increasing inclusion of the second echo with a decrease in depth (see Fig. 3). By 4 m in depth, both data sets should have included most of the second echo. The sharp increase in EM 1 just below 3 m in the RV *Pallasi* 2004 data set, at the shallowest depth, may indicate partial inclusion of the third echo. Thus accidental analysis of more than one echo with QTC IMPACT can cause strong depth-related influences and can create significantly different echogram measurements such that additional substrate classes could be created. To avoid such problems, users need to compare the depth range for their echogram measurement analysis (echo envelope) to the range of depths in their study area.

Conclusions

The need for a cost-effective approach to classify seafloor substrates, in order to define EFH across areas such as the NMFS bottom trawl surveys of the Gulf of Alaska and Aleutian Islands, remains strong. Because of the unexpected problems with the QTC IMPACT processing steps and creation of EMs, it seems highly likely that QTC IMPACT users are producing substrate classifications based on problems implementing the software or analyzing the measurements. Although data-gathering or data-processing errors are common across all such analyses, there is little chance to correct such errors when using a black box system. Therefore for future projects more transparent analytical methods will be needed, such as the published algorithms in Kloser et al. (2001) and van Walree et al. (2005), for translating acoustic data into EFH.

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Age-specific movement patterns of sablefish (*Anoplopoma fimbria*) in Alaska

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Abstract—Over 34,000 age 0–2 juvenile sablefish (*Anoplopoma fimbria*) were tagged and released in southeast Alaska waters during 1985–2005. The data set resulting from this tagging study was unusual because of its time span (20 years) and because age could be reliably inferred from release length (i.e., tagged and released fish were of known age); thus, age-specific movement patterns could be examined. The depth- and area-related recovery patterns supported the concepts that sablefish move to deeper water with age and migrate counterclockwise in the Gulf of Alaska. Availability to the fishery increased rapidly for fish of younger ages, peaked at age 5 to 6, and then gradually declined as sablefish moved deeper with age. Decreased availability with age may occur because of lower fishing effort in deep water and could have substantial implications for sablefish stock assessments because "dome-shaped" availability influences the reliability of abundance estimates. The area-related recovery pattern was not affected by year-class strength; i.e., there was no significant density-dependent relationship.

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The general migration pattern of sablefish (*Anoplopoma fimbria*) in the northeast Pacific Ocean was deduced in the 1980s from several tagging studies (Bracken, 1983; Beamish and McFarlane, 1988; Fujioka et al., 1988;) and enlarged upon in further studies over the following two decades (Heifetz and Fujioka, 1991; Rutecki and Varosi, 1997; Kimura et al., 1998; Maloney, 2004). In southeast Alaska, juvenile sablefish that are spawned offshore appear in inshore waters in late summer or early fall and spend the first year or two of life in shallow coastal bays and inlets before moving into progressively deeper water. At the same time that they are moving into deeper water, many young sablefish move north and west on a migration path that takes them across the Gulf of Alaska to the Aleutian Islands and Bering Sea. Eventually, most will return to the eastern Gulf of Alaska as adults.

The sablefish fishery in the Gulf of Alaska (GOA), eastern Bering Sea, and Aleutian Islands is managed by the National Marine Fisheries Service (NMFS) in cooperation with the North Pacific Fishery Management Council. Sablefish in these areas are assumed to belong to one population (Kimura et al., 1998), for which a total allowable catch is calculated each year and apportioned among six management areas. The annual quotas for each area are based on the distribution of biomass among the areas, which is estimated from longline surveys and commercial catches (Heifetz et al., 1997). Because sablefish are known to be migratory, estimates of the rates of migration between areas could affect the apportionment of quotas among management areas (Heifetz et al., 1997).

Migration rates between areas have been estimated from tag data by using fish-length classes in the modeling process (Heifetz and Fujioka, 1991). Although fish-length data are commonly available, actual age data are generally scarce. Age data are preferable to length data for estimating population age structure (Sigler, 1999), but sablefish are difficult to age, especially for ages greater than 5 or 6 years (Kimura and Lyons, 1991). Tagging of known-age juveniles before they leave coastal areas offers an opportunity to document age-specific movements. Age 0–2 (mostly age 1) sablefish have been tagged annually since 1985 in bays and inlets of southeast Alaska. The objective of our study was to determine movement patterns of sablefish based on these known-age fish, using a unique 20-year data set of age-specific mark-recapture data. Specifically, we determined 1) how the depth inhabited by sablefish changes with age; 2) how the area inhabited changes with age; 3) how availability to the primary fishery (longline) changes with age; and 4) whether there is a density-dependent effect of year-class strength on the extent of migration of young sablefish. Results of objectives 1 and 2 largely confirmed the results of previous studies, whereas objectives 3 and 4 were new.

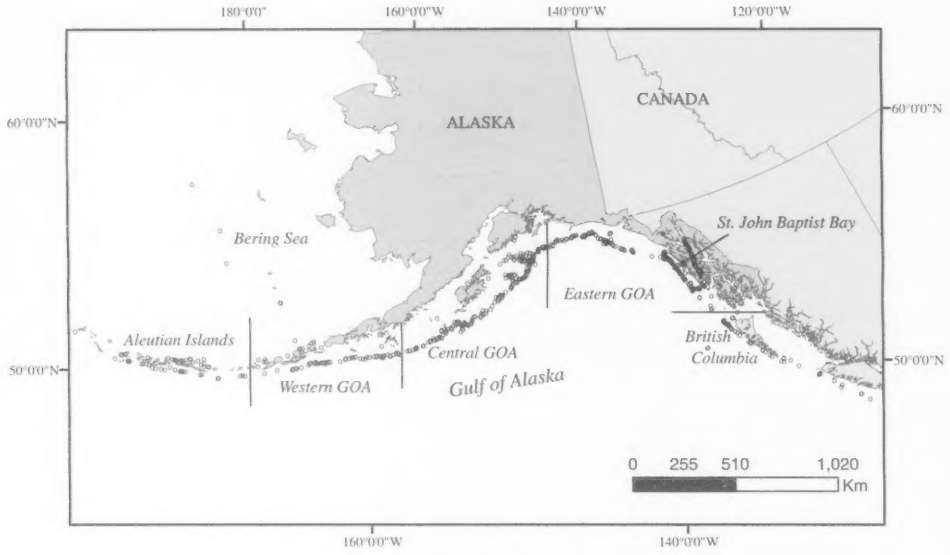

Figure 1

Recovery locations (○) of sablefish (*Anoplopoma fimbria*) tagged and released as juveniles in southeast Alaska. St. John Baptist Bay was the most common release site. Vertical and horizontal bars are regulatory area boundaries. Gulf of Alaska is shown as GOA for the Western, Central, and Eastern areas.

Materials and methods

Juvenile sablefish were captured, primarily with jigging gear (Rutecki and Varosi, 1997) in various bays and inlets of southeast Alaska, for tagging and release from 1985 to 2005. A total of 74 sites were selected during that period, but most tagging after 1987 was undertaken in St. John Baptist Bay near Sitka, Alaska (Fig. 1), because it was easily accessible and juvenile sablefish were consistently found there. Bottom depth is about 30 m and fish were caught on the bottom and throughout the water column. Release and recovery data for these fish are maintained in the NMFS Alaska Sablefish Tag Database, which is described in detail by Fujioka et al. (1988).

Data criteria

Recovered fish had to meet several criteria to be included in this study: recovery year had to be known, recovery depth and location had to be accurate, and the fish had to be at liberty for at least one year. Recovery year was necessary to calculate age at recapture. Accurate recovery depth and location were necessary to reliably assign recovery depth strata and areas. Only recoveries for which there were reported positions that were precise to within 10 minutes of latitude and longitude were used; this criterion was used to judge the reliability of the recovery information. Some tag recoveries had accurate recovery location but no depth information; these tag recoveries were included in the area analysis, but not the depth analysis. Recovery depths were classified into seven depth strata chosen to reflect general habitat type: 1–100 m (nearshore), 101–200 m (continental shelf), 201–300 m (shelf break), 301–500 m (upper continental slope), 501–700 m (middle slope), 701–1000 m (lower slope), and >1000 m (deep water). Recovery locations were classified into seven areas: Aleutian Islands, Bering Sea, western Gulf of Alaska (western GOA), central Gulf of Alaska (central GOA), eastern Gulf of Alaska outside waters (eastern GOA outside), eastern Gulf of Alaska inside waters (eastern GOA inside), and British Columbia. For some analyses, inside and outside waters were pooled and referred to as eastern GOA. The minimum time at liberty of one year was imposed to exclude short-term movements and to focus on migration.

Age at release was determined from fish size and time of year. Depending on the time of year, in most years and tagging areas, no more than two ages of fish, and usually only one, were present at the time of tagging. Ages were readily separable by means of non-overlapping length frequencies and by time of year. Age-0 fish enter into bays from the ocean in the fall of their first year of life, and they average 21–23 cm in length (Rutecki and Varosi, 1997). One-year-old fish in the middle of summer average 31–35 cm and 2-year-old fish average 40–45 cm. The number of years at liberty after release was calculated by subtracting the release year from the recovery year; adding this number to the release age supplied the recovery age.

Availability to the fishery by age

Sablefish move progressively deeper with age, and as they do so, become available to the main commercial fishery (longline), which operates primarily on the continental slope. The fraction of the total population available by age to the commercial fishery was estimated by the following method. The initial number of tagged fish released in year t of age a is N'_{at}. A fraction of the tags, $l = 0.048$ (Lenarz and Shaw, 1997), are immediately lost or the fish die from tagging, such that a short time after tagging, some smaller number of tagged fish survive,

$$N_{at} = (1 - l)\, N'_{at}.$$

The year following tagging, the number of tagged fish is

$$N_{a+1,t+1} = N_{at} \exp\left(-(M + \lambda s_a F_t + H)\right),$$

where M = 0.1 (Sigler, 1999; Hanselman et al., 2006) is the instantaneous rate of natural mortality;

λ = a calibration parameter (Heifetz and Fujioka, 1991) to account for bias in assumed values for the instantaneous rates of annual fishing mortality (F_t);

s_a = availability (selectivity) to the commercial fishery; and

H = 0.03 (Lenarz and Shaw, 1997) is the instantaneous rate of tag shedding.

The F_t values were estimated independently in the Alaska sablefish stock assessment (Hanselman et al., 2006). The fishery captures a number of the tagged fish, C_{at}, where

$$C_{at} = \lambda s_a F_t / (M + \lambda s_a F_t + H) \left(1 - \exp\left(-(M + \lambda s_a F_t + H)\right)\right) N_{at}.$$

The relationship between availability and age was represented by the exponential-logistic function (Thompson, 1994; Sigler, 1999)

$$s_a = 1 / (1 - \gamma)\left((1 - \gamma) / \gamma\right)^{\gamma} \exp\left(\beta\gamma(\alpha - a)\right) / \left(1 + \exp\left(\beta(\alpha - a)\right)\right).$$

The exponential-logistic function is flexible, allowing both asymptotic availability when availability increases with age to an asymptote, and dome-shaped availability when availability increases with age to a maximum and then decreases for older fish. The exponential-logistic function automatically scales maximum availability to 1.0 and reduces to asymptotic availability as the parameter γ approaches zero. When $\gamma = 0$, the parameter α is the age of 50% availability and the slope of the curve equals ¼ β at $a = \alpha$. When $\gamma > 0$, then α and β lose biological meaning because α no longer represents the age at 50% availability, and γ is a parameter that allows availability to decrease (and form the "dome-shape") for older ages The fishery switched from open access to individual fishing quotas (IFQ) in 1995. This switch has been shown to affect availability of the fish to the fishery (Sigler and Lunsford, 2001). Thus, we estimated availability parameters, α, β, and γ, as well as the fishing mortality calibration parameter, λ, separately for each time period (1984–94, 1995–2005). We assumed that the estimated availability curves represent the commercial longline fishery because most tags (93%) were recovered by longline or other fixed gear types.

Not all tagged fish caught in the sablefish fishery are reported (Heifetz and Maloney, 2001). The number of tags reported, R, is related to the number of tagged fish caught, C_{at}, where $R_{at} = w_t\, C_{at}$ and w_t is the reporting rate. Heifetz and Maloney (2001) estimated annual reporting rates for 1980–98 and subsequent reporting rates were estimated of 0.43 for 1999–2001 and 0.52 for 2002–05, which we applied in our analysis.

The model parameters (α, β, γ, and λ for 1984–94 and 1995–2005) were estimated by maximum likelihood. The observed number of tag recoveries in any year-cohort grouping was small (mean of 6, range of 0 to 27); therefore the expected number of tag recoveries, Q, could be approximated by the Poisson distribution (Hilborn, 1990). The negative log-likelihood ($-\log_e L$) for all observed recoveries was

$$-\log_e L(Q_{at} | R_{at}) = \sum_a \sum_t \left(Q_{at} - R_{at} \log_e(Q_{at}) + \log_e(R_{at}!)\right),$$

which was minimized to find the most likely set of parameter estimates. We examined model fit using deviance (McCullagh and Nelder, 1983), which for any observation of tag recoveries is

$$deviance(a,t) = -2\left\{\log_e L(Q_{at} | R_{at}) - \log_e L(R_{at} | R_{at}\right\}$$

(Heifetz and Fujioka, 1991). We applied the likelihood ratio test for nested models (Hilborn and Mangel, 1997) to determine whether model fit was significantly improved by assuming separate parameter sets for the open access and IFQ fisheries. We estimated the 95% confidence intervals of the parameters from their likelihood profiles (Hilborn and Mangel, 1997).

Density-dependent effect on migration

Migration may be affected by abundance if sablefish tend to disperse when abundant. We tested for a density-dependent effect by examining whether recovery patterns by area were influenced by cohort abundance (recruitment strength). Recruitment strength is estimated through age-structured population modeling (Hanselman et al., 2006) and is expressed as the number of fish at age 2 (in millions). We tested by linear regression whether more recoveries occurred in western areas for stronger year classes, hypothesizing that more mem-

Table 1

Total numbers of juvenile sablefish (*Anoplopoma fimbria*) released and recovered in southeast Alaska, 1985–2005, by release age (age 0, age 1, and age 2). Also shown are numbers of recoveries of fish with known recovery year, with accurate recovery location and accurate recovery depth, for fish at liberty longer than one year.

Year	Age 0	Age 1	Age 2	Total releases	Total recoveries	Accurate recovery location	Accurate recovery depth
1985	0	6168	0	6168	853		
1986	0	240	936	1176	68	2	1
1987	0	7916	0	7916	314	8	7
1988	1762	2142	1	3905	153	26	20
1989	0	530	1	531	35	47	41
1990	0	0	0	0	0	65	53
1991	789	2580	1	3370	154	56	39
1992	0	1658	0	1658	68	57	47
1993	0	568	26	594	48	66	59
1994	0	1190	8	1198	44	31	27
1995	0	986	0	986	75	50	42
1996	0	1735	0	1735	62	46	42
1997	0	58	0	58	4	59	55
1998	0	1174	0	1174	37	43	38
1999	0	859	5	864	41	61	56
2000	0	559	178	737	41	40	31
2001	0	105	1	106	3	41	34
2002	0	471	2	473	8	37	29
2003	766	0	0	766	0	56	49
2004	0	290	1	291	0	40	34
2005	0	610	0	610	3	29	26
Totals	3317	29,839	1160	34,316	2011	860	730

bers of strong year classes would move westward if cohort density affected migration.

Results

Over 34,000 juvenile sablefish were tagged and released in southeast Alaska from 1985 to 2005 (Table 1). Most (87%) were tagged and released at age 1. A total of 2011 sablefish tagged as juveniles were recovered, most by the commercial fishery and a few by research vessels. Of these 2011 recoveries, 860 fish had a known recovery year, accurate recovery information, and were at liberty for at least one year, thus qualifying for area-based analyses; 730 fish also had known recovery depth and qualified for depth-based analyses (Table 1). Of the 860 fish recovered, most (85%) were caught by longline, 8% by pots, 6% by bottom trawl, and the remainder (1%) by jig, purse seine, sport fishing gear, or by unknown gear. The largest percentage (45%) of recoveries occurred in the eastern Gulf of Alaska (Table 2). Large percentages of tagged fish also were recovered in the central Gulf of Alaska (30%) and farther westward (18%). About half (51%) of recoveries occurred at depths 501–700 m and nearly all (93%) recoveries occurred at depths from 201 to 1000 m.

Sablefish tagged as juveniles in southeast Alaska were recovered as far west as 177°E along the Aleutian Islands, as far north as 60°N in the eastern Bering Sea, and as far south as 48.5°N off Vancouver Island (Fig. 1). Most recoveries were located along the upper continental slope or in cross-shelf gullies such as Spencer and Seward Gullies. Having originated in coastal bays, these fish had to cross the continental shelf to reach these areas. Fish recovered in Chatham Strait may have moved there by way of inland waters or may have migrated first to outer coastal waters before moving into the strait.

Recovery locations by depth and area

Generally, young fish were more common at shallower depths and older fish were more common at greater depths. In depths shallower than 200 m, the most common ages of tagged juvenile sablefish recoveries were 3 and 4 years, and in depths greater than 200 m, the most common ages were 5–8 years (Fig. 2). Median recovery age increased with depth from shallow (2 years)

Table 2

Recovery area and depth strata (m) for recovered sablefish (*Anoplopoma fimbria*) tagged as juveniles, number of fish for which depth was unknown, and total number of tagged fish captured in the recovery area. Proportion of recoveries at depth (bottom row) excludes recoveries with unknown depth. Proportion of recoveries by recovery area (rightmost column) includes recoveries with unknown depth. GOA = Gulf of Alaska.

	Depth strata (m)									
Recovery area	1–100	101–200	201–300	301–500	501–700	701–1000	>1000	Unknown	Total	Proportion
Bering Sea				4	9	4		1	18	0.02
Aleutian Islands		3		5	39	7		8	62	0.07
Western GOA		4	6	19	28	7		10	74	0.09
Central GOA		25	43	48	90	19	2	28	255	0.30
Eastern GOA	2	12	8	67	177	45	1	75	387	0.45
British Columbia			6	11	26	12	1	8	64	0.07
Total	2	44	63	154	369	94	4	130	860	
Proportion	0.00	0.06	0.09	0.21	0.51	0.13	0.01		730	

to deep (5–6 years). Only two 2-year-old sablefish that had traveled <6 km from their release location in St. John Baptist Bay were recovered in nearshore waters (<100 m water depth); no fish older than 2 years were recovered in nearshore waters. Only one sablefish older than 13 years was found in depths <300 m and most were found deeper than 500 m.

The most common areas of recovery were the central GOA and the eastern GOA, which together accounted for 75% of all recoveries (Table 2). There were more than twice as many recoveries in outside waters as in inside waters of the eastern GOA. The most common ages of recovered fish in all areas except eastern GOA and British Columbia were 5 to 7 years (Fig. 3). In eastern GOA the most common ages at recovery were 3 to 6 years, and in British Columbia 6 to 9 years. Fish of all ages from 3–10 years old were recovered in all areas except the Bering Sea, where no fish younger than 4 years old were recovered. The Bering Sea had the fewest recoveries (only 18) and the smallest range of ages (4–10 years, except for one recovery of a 19-year-old fish). Most fish 2 years old and most fish older than 12 years were recovered in the eastern GOA (Fig. 3). Most recoveries in western areas (Bering Sea, Aleutian Islands, western Gulf of Alaska) were 12 years old or less. The large number of recoveries that occurred in the central Gulf of Alaska (30%) and farther west (18%) indicated that nearly half of the population had moved westward from the eastern Gulf of Alaska (Table 2).

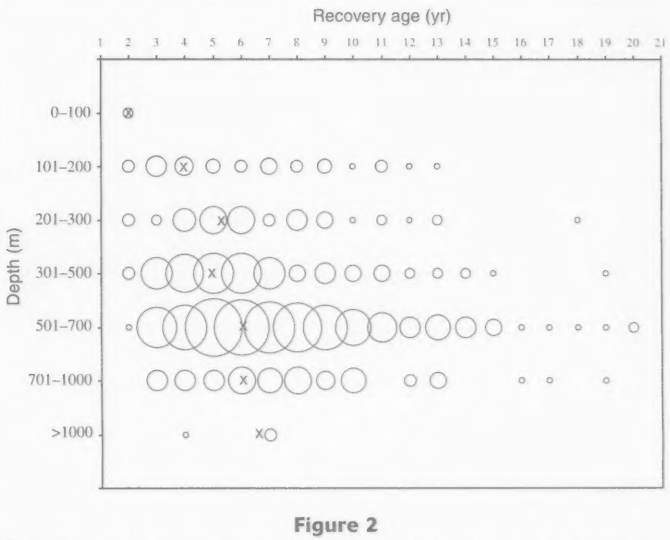

Figure 2

Tag recoveries from sablefish (*Anoplopoma fimbria*) tagged as juveniles, by age (years) and depth (m) for all areas pooled. The size of the circles is proportional to the number of recoveries and represents a range from 1 to 57 recoveries. The symbol (×) represents the median age (years).

Movement by age

Age-specific movement patterns were discernible even though multiple ages were found within areas and depths. By ages 3 and 4 years, most fish had moved offshore into >100 m water depth (Fig. 2). Some had moved to the inside waters of the eastern GOA or directly south into the waters off British Columbia, but most were found in eastern GOA outside waters or in the central GOA

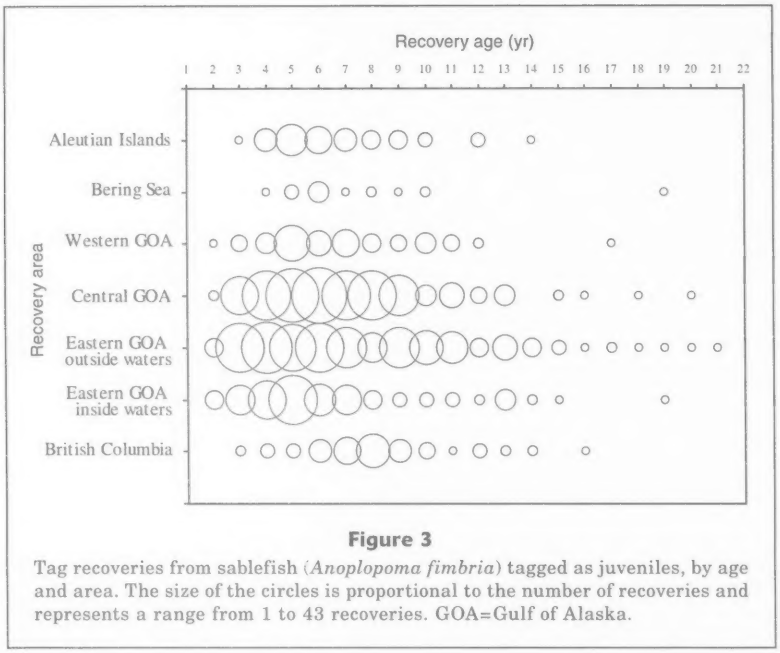
Recovery age (yr)
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22
Recovery area
Aleutian Islands
Bering Sea
Western GOA
Central GOA
Eastern GOA outside waters
Eastern GOA inside waters
British Columbia

Figure 3

Tag recoveries from sablefish (*Anoplopoma fimbria*) tagged as juveniles, by age and area. The size of the circles is proportional to the number of recoveries and represents a range from 1 to 43 recoveries. GOA=Gulf of Alaska.

(Fig. 3). By ages 5 and 6 years, many fish had reached the western areas. Age 5 was the most common age of recovery for the western GOA and Aleutian Islands, and age 6 for the Bering Sea. Some fish aged 7–9 years remained in the western areas, but most had begun a return to the east. In the central GOA and eastern GOA outside waters, the 7–9-year-olds were mostly found in the 501–700 m depth range and were some of the most numerous fish. Fish aged 6–9 years were the most commonly recovered in the waters off British Columbia and may also have been fish returned from a westward migration (Fig. 4). A few fish may have come from eastern GOA inside waters (Chatham Strait), but Maloney and Heifetz (1997) found that this area has a high proportion of non-migrating fish. The most common depth stratum for fish recovered in British Columbia was the 501–700 m stratum.

Availability to the fishery by age

The model of availability at age fit the observed pattern of tag recoveries well. Deviances were scattered symmetrically around zero for most ages (Fig. 5). Only for ages 2 and 13 were there noticeable biases. The full model that assumed separate selectivity functions for the open access and IFQ fisheries significantly improved model fit, compared to a single selectivity function (Likelihood ratio test, χ^2=220.1, df=3, P<0.001). The assumption of separate calibration coefficients rather than a single calibration coefficient also significantly improved fit (likelihood ratio test, χ^2=189.7, df=1, P<0.001). Including parameters to allow availability to decrease for older ages (γ for 1985–94 and 1995–2005) significantly improved fit compared to a reduced model with asymptotic availability (likelihood ratio test, χ^2=686.7, df =2, P<0.001).

Juvenile sablefish first became available to the commercial fishery at age 2. Availability rapidly increased such that by age 5, nearly all sablefish were available to the commercial fishery (Fig. 6). Both the age at 50% availability and the age at 100% availability values were one year greater (older) in the IFQ fishery than in the open access fishery (4 years versus 3 years and 6 years versus 5 years, respectively). Availability decreased for older ages, such that by 15 years, availability was 50% for the open access fishery and 20% for the IFQ fishery. The degree of dome shape was sensitive to the assumed value of M; for example, by 15 years, availability for the open access fishery was 70% for M = 0.12 compared to 50% for the assumed value of M = 0.10.

Density-dependent effect on migration

We tested whether year-class strength affected the proportion of recoveries in the western areas, hypothesizing that a density-dependent effect would cause more recoveries in western areas for strong year classes. There was no significant relationship (regression, df=14, P=0.18) because about 20% of recoveries occurred in western areas, regardless of year-class strength (Fig. 7). In the regression, the proportion was transformed by arcsin squareroot, as is recommended to normalize data expressed as proportions (Zar, 1984).

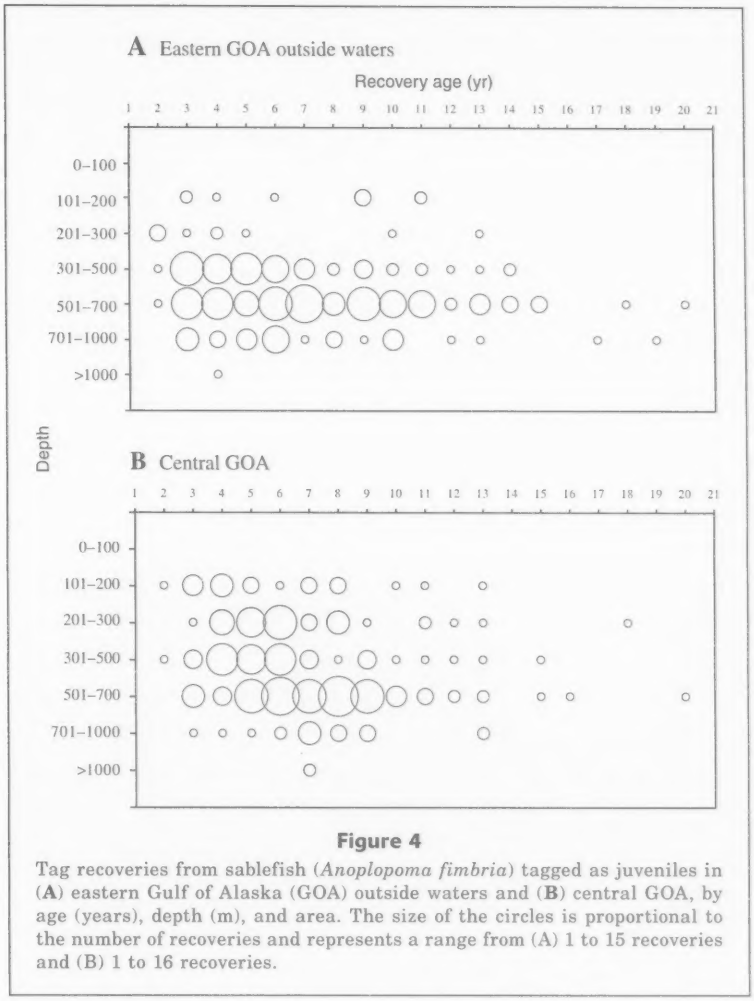

Figure 4

Tag recoveries from sablefish (*Anoplopoma fimbria*) tagged as juveniles in (**A**) eastern Gulf of Alaska (GOA) outside waters and (**B**) central GOA, by age (years), depth (m), and area. The size of the circles is proportional to the number of recoveries and represents a range from (A) 1 to 15 recoveries and (B) 1 to 16 recoveries.

Discussion

Movement by depth and area with age

Sablefish spend 1–2 years nearshore before moving onto the continental shelf where they reside as adults and spawn. In this study, the most common ages in the shallower depths were 3–4 years and in the deeper depths 5–8 years, indicating that sablefish are younger on the continental shelf than on the continental slope. This result confirmed other sablefish age data that indicated that fewer sablefish older than 10 years are found on the continental shelf than on the continental slope (Sigler et al., 1997). Concurrent with the offshore movement with age, many young fish from the eastern areas (British Columbia, eastern GOA) moved in a northerly and westerly direction through the central GOA to the western areas (western GOA, Bering Sea, and Aleutian Islands). The simultaneous depth and area movements resulted in a general age distribution of younger fish in shallower water in the east, mid-age fish in middle depths in the west, and older fish in deeper waters on the return from western to eastern areas.

Age pattern variability was high; there was a substantial overlap of ages within and between depths and areas. For example, fish of ages 2–13 years were recovered in 101–200 m and fish aged 2–20 years were caught in 501–700 m. Likewise, fish of all ages from 3 to 10 years were recovered in all areas except the Bering Sea where the youngest fish recovered was 4 years old. However, the separation of ages by depth, although incomplete, was quite pronounced within some areas, most notably the eastern GOA outside and the central GOA (Fig. 4). In both of these areas the distribution of younger fish in shallower water and older fish in deeper water was evident and, taken together with the general

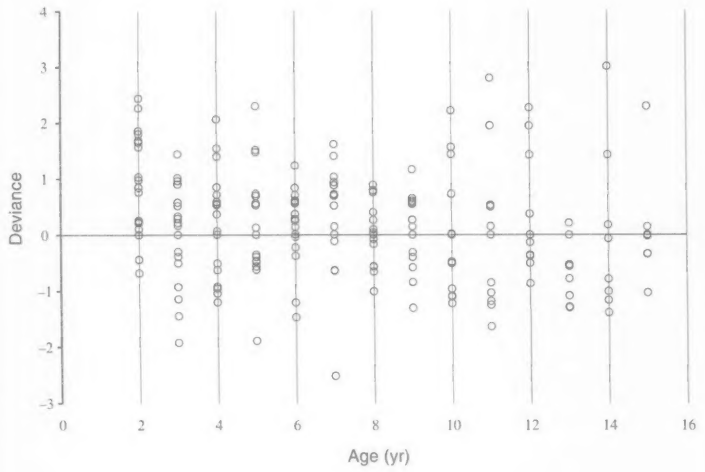

Figure 5

Scatterplot representing the fit of observed and predicted availability of sablefish (*Anoplopoma fimbria*) to the fishery by age. Deviance is a function of the difference between observed and predicted values; a smaller deviance indicates a better fit of the exponential-logistic model to the observation.

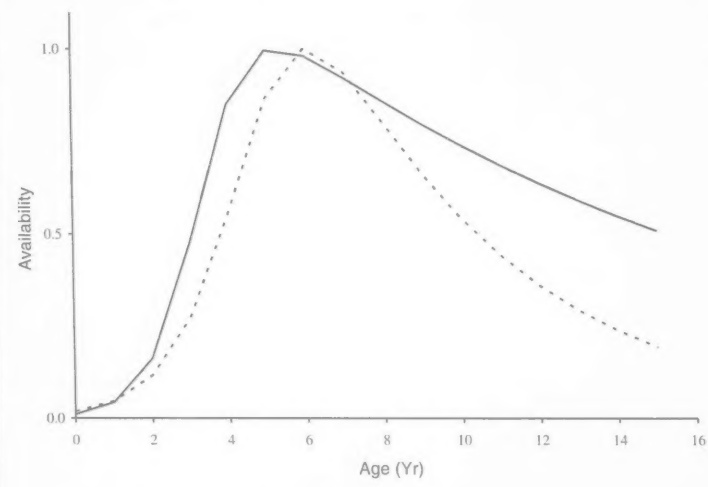

Figure 6

Estimated availability (fraction of the total population) of sablefish (*Anoplopoma fimbria*) to the fishery by age (years) for the open-access (1985–94, ———) and individual fishing quota (IFQ) (1995–2005, ----) fisheries. Parameter estimates and 95% confidence intervals for 1985–94 are $\alpha = 1.50$ (1.26, 1.87), $\beta = 3.33$ (3.04, 3.69), $\gamma = 0.050$ (0.023, 0.092), and $\lambda = 0.23$ (0.22, 0.25) and for 1995–2005 are $\alpha = 1.14$ (1.05, 1.24), $\beta = 4.76$ (4.53, 5.01), $\gamma = 0.18$ (0.15, 0.21), and $\lambda = 0.38$ (0.36, 0.39).

age distribution by area, corroborated the counterclockwise pattern of sablefish migration in the northeast Pacific Ocean.

Availability to the fishery by age

The pattern of movement from shallow to deep water with age (Fig. 2) results in increased availability to the fishery as sablefish grow older (Fig. 6). Estimates of availability at age have shown that about half of sablefish are available to the fishery by age 3 or 4, depending on the fishery management system, and that most are available by age 5 or 6. The later availability of fish (at ages 5 or 6) under the IFQ management system (compared to earlier availability of younger fish under the open access system) also was also found to be the case in an analysis of length-frequency data from the two fisheries, and this pattern of availability was likely created because the crowding of fishing vessels during the open access fishery pushed fishermen into areas and depths where there were smaller fish (Sigler and Lunsford, 2001). The IFQ fishery, with a longer season and fewer vessels, reduced crowding so that fishermen were able to avoid shallower depths with smaller, younger fish.

Unlike previous analyses, where availability was assumed not to decrease with age (e.g., Sigler, 1999), our analysis of known-age tag recoveries showed that sablefish availability decreases with age. An alternate explanation is that tag loss increased with time. However, double-tagging experiments have shown that the rate of tag loss is constant with time (Beamish and McFarlane, 1988; Lenarz and Shaw, 1997). Decreased availability with age may occur because of reduced fishing effort for older age fish. Fishing effort is concentrated at intermediate depths (e.g., half of the recoveries occurred at depths 501–700 m [Table 2]) but fish exit these depths as they age and move deeper. In addition, older fish were less available for IFQ management compared to open access management, which also may have been due to reduced crowding of fishing grounds during IFQ man-

agement; for example, recoveries at depths >700 m were fewer during IFQ management (16% of recoveries during 2003–05) than during open access management (25% during 1992–94). This result has potentially substantial implications for a stock assessment because "dome-shaped" availability influences the reliability of abundance estimates (Bence et al., 1993; Sigler, 1999). A logical next step for other researchers to understand these effects is to complete a migratory catch-age analysis (e.g., Quinn et al., 1990) that melds sablefish migration (Heifetz and Fujioka, 1991) and age-structured (Sigler, 1999; Hanselman et al., 2006) analyses.

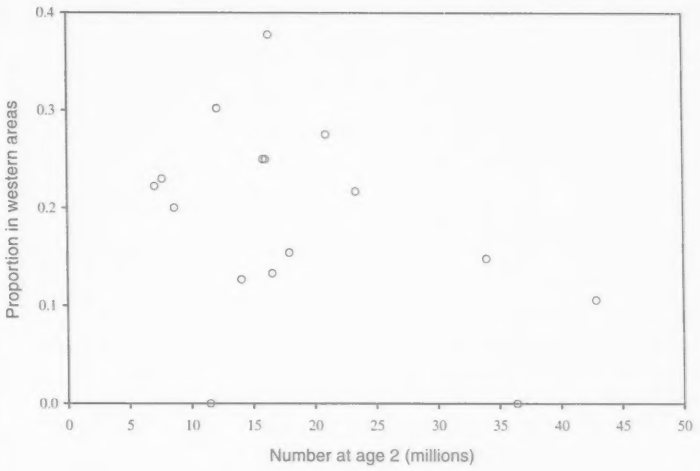

Figure 7

Scatterplot of proportion of sablefish (*Anoplopoma fimbria*) tag recoveries in western areas (Bering Sea, Aleutian Islands, Western Gulf of Alaska) versus year-class strength (number at age 2 in millions; Hanselman et al., 2006).

Density-dependent effect on migration

Migration is a prominent feature in the life history of many fishes. Well-known examples of migratory fish are Pacific salmon (*Oncorhynchus* spp.) that return to their natal stream to spawn (Burgner, 1991; Heard, 1991) and Pacific herring (*Clupea harengus*) that consistently follow routes from spawning to feeding grounds (Hourston, 1982; Wheeler and Winters, 1984; Corten, 2002). Presumably the energy expended during migration is compensated for by other benefits. Demonstrated benefits include the ability to take advantage of seasonally available prey (Walters et al., 1986; Livingston, 1993) and avoidance of predation (Carlson, 1980). Benefits of migration for sablefish are not immediately obvious because they are opportunistic feeders and have no need to pursue specific prey, and their rapid growth rate in early life quickly lessens their vulnerability as prey. Nevertheless, a substantial proportion of the population migrates each year (Heifetz and Fujioka, 1991; Kimura et al., 1998).

Sablefish are characterized by great variability in year-class strength; and occasional strong year classes dominate the fishery for several years in a row (Sigler, 1999; Hanselman et al., 2006). A higher proportion of a strong year class may migrate and young fish may move farther and faster in order to occupy less crowded areas (density-dependent habitat selection; e.g., MacCall, 1990). Beamish and McFarlane (1988) noted differing rates of sablefish movement out of release areas from 1977 to 1985 and theorized that increased density resulting from recruitment of the large 1977 year class may have contributed to an increased rate of movement. However, we found no significant effect of year-class strength on the proportion of recoveries in the western areas, and therefore cohort density does not appear to affect the proportion of a cohort that will migrate. Although we tested a long time series, this time series does not span the full range of observed recruitment variability. Some earlier year classes were substantially stronger (e.g., the exceptional 1977 year class was 44% larger than the strongest year class (1984) that we tested). Migration may be stronger for year classes of such magnitude. Further, movement rates may be affected by total abundance—a possibility that could be tested in a sablefish migratory catch-age analysis such as we suggested earlier.

Observed sablefish abundance trends by area during the last 25 years can be explained by their counterclockwise migration pattern. Overall sablefish abundance peaked in the late 1980s and then decreased. The western areas of Bering Sea, Aleutian Islands, and western GOA decreased quickest, as migrating fish matured and turned eastward (Fig. 8). Abundance declined more slowly in the eastern GOA, presumably because fish that migrated westward returned to the eastern GOA. The abundance decline in the central GOA was intermediate, probably because migrating fish pass through in both directions (westward and eastward). This pattern of abundance changes (faster in western areas, slower in central and eastern GOA) supports the conclusion that the eastern GOA and the eastern part of the central GOA are the center of the range for Alaska sablefish (Bracken, 1983; Beamish and McFarlane, 1988; Sigler et al., 2001).

Currents and sablefish migration

Prevailing currents may play an important role in determining the direction of migration for most young sable-

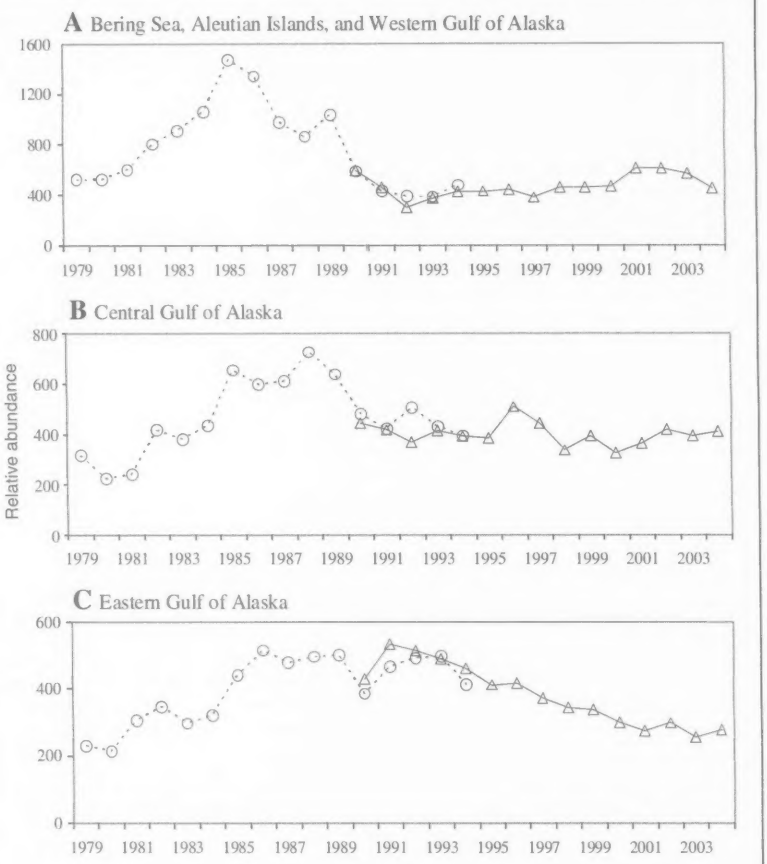

Figure 8

Relative abundance (weight) from sablefish (*Anoplopoma fimbria*) longline surveys, 1979–2004: Japan-U.S. cooperative longline survey (○) and U.S. (domestic) longline survey (△) (Hanselman et al., 2006). The values for the U.S. survey were adjusted to account for the higher efficiency of the U.S. survey gear.

fish. From the time they first venture out of coastal bays onto the continental shelf of northern British Columbia or the eastern GOA, young fish are subject to northward or westward flowing currents. Driven by fresh water runoff, the Alaska Coastal Current (ACC) flows northwestward close to shore toward the head of the Gulf of Alaska (Royer, 1981). From Icy Bay at about 137°W the ACC flows 1500 km to Unimak Pass at the eastern end of the Aleutian Island chain (Stabeno et al., 2004). This inshore current is likely the initial route of most young sablefish leaving nursery areas in southeast Alaska. As the fish move westward, cross-shelf gullies and canyons provide avenues of deeper water leading to the shelf break and the upper continental slope, along which runs the westward-flowing Alaskan Stream. The potential ease of transit from the Alaska Coastal Current on the shelf to the Alaskan Stream on the upper slope may help to explain the considerable overlap in fish ages that we found within and between depths.

The direction of migratory movement by young sablefish may be influenced by prevailing current direction, but the return of adult sablefish along the continental slope to the eastern areas of the GOA is presumably made against the westward-flowing Alaskan Stream and from a lower density area to a higher one. Reed and Schumacher (1987) believed that velocities of the Alaskan Stream are low in water deeper than 300 m, and most of the fish travel within a 500–700 m depth when returning; therefore swimming against the current would not pose a problem for adult fish. The return of most adults to the eastern GOA serves to maintain the center of the population there and likely increases the chance of successful spawning in that area.

One factor that may make the eastern GOA and British Columbia spawning grounds more favorable is that spawning depths in these areas are closer to the coast than those farther west because of the narrow continental shelf in much of the eastern GOA. Also, the prevailing north-flowing Alaska Current in the eastern GOA may carry pelagic larvae and young fish closer inshore for easier access to coastal nursery areas. In the central and western GOA, spawning depths are farther offshore, increasing predation risk for larvae, and there is no prevailing northerly current to transport larvae shoreward. Instead, the Alaskan Stream, up to 100 km wide, flows westward along the shelf break, more or less perpendicular to the route that offshore-spawned larval and juvenile sablefish must travel to reach inshore nursery grounds. Tokranov (2002) believes this current is the source of periodic occurrences of juvenile sablefish off Kamchatka and the Kuril Islands. Winter current direction and sablefish recruitment success are related, and above-average recruitment is more likely in years with northerly drift (59%) than for years with an easterly or southerly drift (25%) (Sigler et al., 2001).

All the sablefish in this study originated in the eastern GOA, but young-of-the-year sablefish have been caught in small numbers on various cruises in the Bering Sea, Aleutian Islands, western and central GOA, as well as the eastern GOA from 1955 to 1999 (Kendall and Matarese, 1987; Sigler et al., 2001). These observations indicate the likelihood of some direct recruitment into each of these areas, in addition to recruitment resulting from migration. Spawners contributing to each area may be migrants returning to the eastern GOA, adult fish that are resident in the area, or adult fish in an adjoining upstream area whose larvae are caught up in the prevailing currents and are carried westward. Although most fish in our study older than 12 years were recovered in eastern GOA outside waters, older fish (13 to 21 years) also were recovered in each of the other areas, indicating that they may have become resident in the new area at some point during migration.

Our study corroborated much that is already known or suspected about sablefish migration in Alaska waters. In addition, our data on age by depth and area have refined our knowledge of sablefish movements. Further studies to locate sablefish nursery grounds throughout the GOA and in the Bering Sea and Aleutian Islands and to tag juveniles on these grounds as was done in the eastern GOA for our study would determine whether these movement patterns observed in the present study are similar to movement patterns of sablefish originating in other regions of Alaska.

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Distribution of red deepsea crab (*Chaceon quinquedens*) by size and sex in the Gulf of Mexico

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The red deepsea crab (*Chaceon quinquedens* (Smith, 1879)) has supported a commercial fishery off the coast of New England since the 1970s (Wigley et al., 1975) and has had annual harvests from 400 metric tons (t) (1996) to 4000 t (2001) (NEFMC, 2002). In 2002, a fishery management plan for the northeast fishery on the Atlantic coast was implemented and total allowable catch was reduced to approximately 2500 t (NEFMC 2002). Although there are management plans for the golden crab (*C. fenneri*) and the red deep sea crab for Atlantic coast regions, there is no fishery management plan for red deepsea crabs in the Gulf of Mexico. Successful management for sustainable harvests should be based on a knowledge of the life history of the species, but *C. quinquedens* has been a difficult species for which to obtain life history and abundance information because of its deep distribution.

Previous studies used trap surveys to estimate the relative abundance and distribution of *C. quinquedens* and almost all had similar results (Wigley et al., 1975; Stone and Bailey, 1980; Lockhart et al., 1990; Lindberg and Lockhart, 1993; Waller et al., 1995; Trigg et al., 1997). Typically, *C. quinquedens* is found at depths from 100 to 2000 m (Haefner, 1978; Hastie, 1995) in the western Atlantic Ocean and the Gulf of Mexico (Haefner and Musick, 1974). The largest populations of *C. quinquedens* are found on soft sediments along the continental slope (Lindberg and Lockhart, 1993). Red deepsea crabs typically are found in progressively shallower depths as they increase with size (Wigley et al., 1975; Trigg et al., 1997), and this finding indicates that the megalopae, after settling in deeper water, move up the continental slope as they grow. Bathymetric sexual segregation has been reported for many of the *Chaceon* species, including *C. quinquedens* (McElman and Elner, 1982; Lockhart et al., 1990). Females typically are found in shallower waters than those that males inhabit (Wigley et al., 1975; Lockhart et al., 1990), although females have also been found at depths similar to those of males (Wenner et al., 1987).

In previous studies, *C. fenneri* and *C. quinquedens* were found to have similar distributions. However, most studies in which this comparison was made had relatively larger collections of *C. fenneri* than *C. quinquedens* (Lockhart et al., 1990; Lindberg and Lockhart, 1993). The two congeners may be expected to have similar distribution patterns because of their genetic and morphological similarities; however, assumptions made about the distribution of *C. quinquedens* based on the distribution of *C. fenneri* may lead to inappropriate management strategies. Similarly, populations of crabs in the Gulf of Mexico and Middle Atlantic Bight may use habitat differently and further investigation is warranted (Lockhart et al., 1990). Depth limitations of prior surveys have indicated that juveniles may not have been sampled, as evidenced by the depth-limited NEFSC (Northeast Fisheries Science Center) 400 m surveys from 1964 to 1999 where fewer than six crabs smaller than 7-cm carapace width were captured per tow (Steimle et al., 2001).

Chaceon quinquedens is closely related to *C. fenneri* (Weinberg et al., 2003). However, *C. fenneri* is tan and found at shallower depths than the red *C. quinquedens* (Lockhart et al., 1990; Lindberg and Lockhart, 1993). Commonly, when one species of *Chaceon* is studied, data are extrapolated to other congeners because of a limited sample of those congeners or because data have not yet been collected for the congeners. Most of the life history patterns that have been attributed to *C. quinquedens* have been attributed because of its close relationship with *C. fenneri*. Little or no genetic difference between *C. fenneri* and *C. quinquedens* populations was found in the eastern Straits of Florida and the Gulf of Mexico (Weinberg et al., 2003). The hypothesis was that the distribution of *C. quinquedens* would be similar to the distribution observed for *C. fenneri* in previous studies. To examine this hypothesis, we compared the size distribution and sex distribution of *C. quinquedens* near six shipwrecks at varying depths in the Gulf of Mexico. Because fish communities around these shipwrecks were being examined at the time, we took the opportunity to explore red deepsea crab distributions.

Materials and methods

From July 29 to August 16, 2004, six World War II era shipwrecks were surveyed with the remotely operated vehicle (ROV) XL-11 deployed from the HOS *Dominator* in the Gulf of Mexico. The shipwrecks were located

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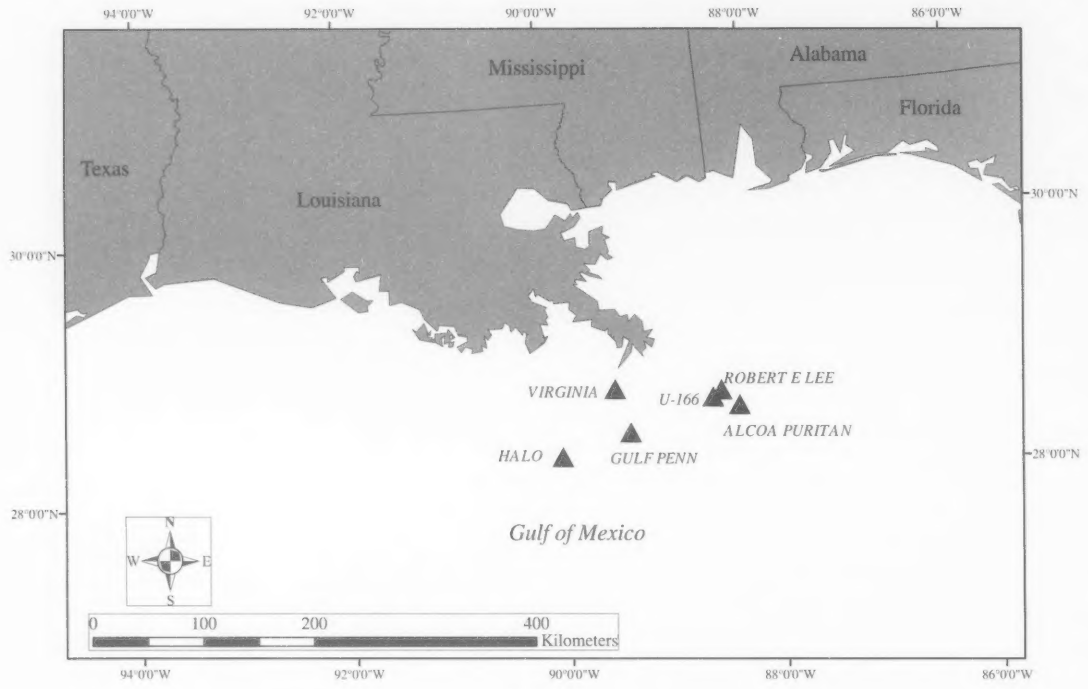

Figure 1

The locations of the shipwreck sites surveyed in the Gulf of Mexico with the XL-11 ROV. Red deepsea crabs (*Chaceon quinquedens*) were found at the four deeper sites (*Gulf Penn, U-166, Robert E. Lee,* and *Alcoa Puritan).*

in the Mississippi Canyon or adjacent areas (Fig. 1) and varied in water depth from 90 to 1970 m. At each wreck, ROV transects were conducted over the wreck and over the debris field. Once transects were completed, traps were set and biological sampling with the ROV began. Transects over the wreck and in parallel lines adjacent to the wreck until about 300 m were mapped before the deployment of the ROV. The ROV and trap sampling time lasted a minimum of eight hours and a maximum of sixteen hours. At each wreck, both a small baitfish trap (95 cm width × 75 cm length × 50 cm height) and a chevron fish trap (150 cm width × 180 cm length × 60 cm height) baited with herring and squid were set within a few meters of the wreck and approximately 300 m away from the wreck. A baited crab trap (64 cm width × 97 cm length × 51 cm height) was placed near the wreck, and two minnow traps (23 cm diameter × 44 cm length) bound together were placed far from the wreck; both were baited with canned cat food and biolume sticks. Additional collections were made at the direction of biologists using the manipulator arm of the ROV for larger invertebrate specimens and the suction hose of the ROV (approximately 10 cm in diameter) for smaller invertebrate specimens.

Each crab specimen collected was measured from the anterolateral spine on one side of the carapace to the anterolateral spine on the opposite side for carapace width (CW) to the nearest 0.1 mm with vernier calipers. Shell condition and missing appendages were noted and sex was recorded. If the crab was female, presence and color of eggs were also recorded. Voucher specimens from each wreck were either preserved in 90% ethanol or frozen.

Statistical analyses were performed with SPSS 14.0 (SPSS, Inc., Chicago, IL) software to determine if crab size or sex was related to the distribution of the crabs. To determine if there was a correlation with size and depth, a linear regression was performed with a 95% confidence interval. To examine the relationship of sex with depth, the Kruskal-Wallis test was used because the data were non-normal. Data were also non-normal for depth distribution, but linear regression was used to determine if a linear correlation existed.

Results

Chaceon quinquedens was found at the four deepest of the six shipwrecks, and there was no linear distribution of the crabs by sex. A total of 127 specimens was collected at the four sites, with CW ranging from 21.2 mm to 141.1 mm (Table 1). No significant correlation occurred between depth and crab size (R^2=0.051). The smallest crabs were found at the shallowest depth, and

Table 1

Carapace width (mm) and numbers of females and males of red deepsea crab *Chaceon quinquedens* found on four shipwrecks in the Gulf of Mexico.

		Carapace width (mm)			Sex	
Shipwreck	Depth (m)	Average	Minimum	Maximum	Female	Male
Gulf Penn	533	24.1	21.2	31	0	4
Robert E. Lee	1428	95.0	56.5	141.1	27	21
U-166	1428	116.0	61.5	136.5	18	6
Alcoa Puritan	1950	66.5	43.7	120.3	22	26

the largest crabs were found at intermediate depths. The four smallest specimens were collected with the suction arm of the ROV (all at the *Gulf Penn* shipwreck) and one crab was collected with the manipulator arm of the ROV. All other samples were collected in the fish traps. No crabs were collected in the minnow traps, and crabs were rarely observed on the shipwrecks. Although slightly more than half of the crabs were collected close to the shipwrecks (74 ±7 m), insufficient data were collected to compare wreck effects on crab size or sex distribution.

Males and females did not have significantly different distributions. A total of 67 females and 57 males was collected (three of unknown sex collected at the *U-166* site) and no depth pattern could be attributed to sex (Table 1; P=0.059).

Discussion

Previous reports of the distribution of *C. quinquedens* have been contradictory to our findings, which were influenced by the addition of a different sampling technique, the ROV. Without the ROV, the four smallest crabs would not have been observed or collected at the shallowest depth. Red deepsea crabs are typically found on silt substrate, and although their abundance on the shipwrecks was not analyzed in our study, we noted that crabs were rarely found on the shipwrecks (see also Kilgour, 2007).

A strong correlation of crab size with depth has been reported in some studies of *C. quinquedens* (Wigley et al., 1975; Lockhart et al., 1990; Lindberg and Lockhart, 1993; Waller et al., 1995; Trigg et al., 1997), but not in others (Wenner et al., 1987). The variation in results may have been caused either by a temporal variation in sampling, or a sampling bias from gear. In our study, the smallest crabs were found at the shallowest site and this result was contrary to that of previous reports (Lockhart et al., 1990; Lindberg and Lockhart, 1993; Waller et al., 1995; Trigg et al., 1997). A linear relationship between crab size and depth was not observed in our study, but this result may have been due to the ROV collections which were composed of the smallest crabs; crabs of a similar small size were not collected with traps at the same site.

An almost equal ratio of females to males occurred in our study and our sampling did not occur during the reported mating season (Wigley et al., 1975; Haefner, 1978; Biesiot and Perry, 1995). Female *C. quinquedens* were found only at the three deepest sites, whereas males were found at four of the six sites; this finding contradicts that of previous studies where depth segregation by sex was observed (Wigley et al., 1975; Lockhart et al., 1990). Sampling methods to date may have been inadequate because the use of traps has been the primary method for obtaining information for this species. Sampling biases often result in more males being collected, particularly when females are ovigerous, because females tend to avoid traps while brooding eggs (Howard, 1982; McDonald et al., 2004; Taggart et al., 2004). Additionally, sampling bias exists for larger males and for smaller males and females; smaller crabs are less likely to enter traps when large males are present (Taggart et al., 2004). *Chaceon quinquedens* is difficult to study because of its deep distribution; techniques other than trap and trawl sampling may be necessary to accurately understand the movements, spatial distribution, and life history of this species.

The bathymetric distribution of many deepwater crab species is suspect because the methods by which these patterns were determined may be biased. We used two different techniques, an ROV and traps; the bathymetric distribution of *C. quinquedens* was different from that of previous studies where a single sampling technique was used. The best data available are used for fishery management, but many times these data represent sampling techniques that may not provide a complete distribution of the species in question. Our study, in spite of a small sample size, demonstrates the importance of using more than one technique for observing the life history and distribution of a deepwater species to reduce the biases of sampling techniques. Both the ROV and the trap surveys have sampling biases, but in combination, may reveal a more accurate picture of the bathymetric distribution of red deepsea crab. The use of multiple sampling gears to gain knowledge of the life history of deepwater crabs is necessary.

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Catches in ghost-fishing octopus and fish traps in the northeastern Atlantic Ocean (Algarve, Portugal)

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Ghost fishing is the term used to describe the continued capture of fish and other living organisms after a fisherman has lost all control over the gear. Traps may be lost for a variety of reasons including theft, vandalism, abandonment, interactions with other gear, fouling on the bottom (i.e., traps and ropes are caught on rocky substrate), bad weather, and human error (Laist, 1995). Annual trap loss can be as high as 20% to 50% of fished traps in some fisheries (Al-Masroori et al., 2004). Because lost traps can continue to fish for long periods, albeit with decreasing efficiency over time (e.g., Smolowitz, 1978; Breen, 1987, 1990; Guillory, 1993), ghost fishing is a concern in fisheries worldwide.

Few studies on the ghost fishing of lost traps have been carried out in European waters, and there has been no information from southern European waters. Ghost fishing of parlour pots used to catch lobsters and crabs off the south-west coast of the United Kingdom was studied by Bullimore et al. (2001), and Godøy et al. (2003) carried out an experimental study on much larger, deliberately lost pots for red king crab (*Paralithodes camtschaticus*) in Norwegian waters. In both cases the effect of ghost fishing by parlour pots was deemed to be relatively small compared to the effects of other types of traps used in Canadian and American fisheries (Brown and Macfadyen, 2007).

In southern Portugal, pots and traps of various types are among the most widely used gears in the small-scale fisheries. Fishing vessels <9 m (local category) can legally fish up to 500 traps, and coastal category vessels (9–12 m and >12 m in total length) are allowed up to 750 and 1000 traps, respectively. The most widely used traps in the Algarve are 1) metal frame, hard plastic netting, single entry traps for octopus (covo), 2) large, metal frame traps for catching cuttlefish and fish (armadilha), and 3) wire traps (murejona) for catching fish. However, only the covo traps and murejona traps were used in our study.

Under the Common Fisheries Policy and the European Community directive on habitats and species, member states are responsible for local fisheries and are obliged to take measures to minimize or mitigate the negative effects of fishing activity. Concern over the effects of lost gear in European waters has led the European Commission to finance two pan-European projects on ghost fishing. The first project focused only on gill nets and trammel nets (Erzini et al., 1997), and the second project included studies on lost traps in several European areas (Godøy et al., 2003). Here we report the results from one of the studies carried out with two types of traps in the northeast Atlantic (south coast of Portugal) (Fig. 1). The catches of deliberately lost traps were monitored and estimates of the number of trap losses and causes of trap losses were obtained through surveys of commercial fishermen.

Materials and methods

Catches in deliberately lost traps

The main gear used to catch octopus is the octopus trap (covo), a small metal framed trap with a single entrance on the top (Fig. 2). To make escapement more difficult, the entrance is partially blocked by plastic strips that are easy to push through when entering the trap but not when exiting. A total of 60 octopus traps, each baited with two sardines, were deployed on August 11, 1999, at two sites off Faro where normal fishing activities with octopus traps takes place. The depth at one site was 20 m, and 50 m at the other, and both were situated near rocky reefs. At each location 30 traps were deployed, 15 on soft bottom and 15 on rocky bottom. Because the traps set at 50 m were difficult to retrieve with a grapnel from the hard bottom or were all lost within one month after deployment (on soft bottom), an additional 30 octopus traps were deployed at the shallower depth on soft and hard bottom on 18 May, 2000 and were monitored weekly for 14 weeks.

In addition to the 90 octopus traps, 10 fish traps of the murejona type were also deployed on 25 May 2000 at the shallower site (20 m depth) and monitored by scuba divers on a weekly basis for three months. Murejona traps are round, wire traps with a single funnel-shaped

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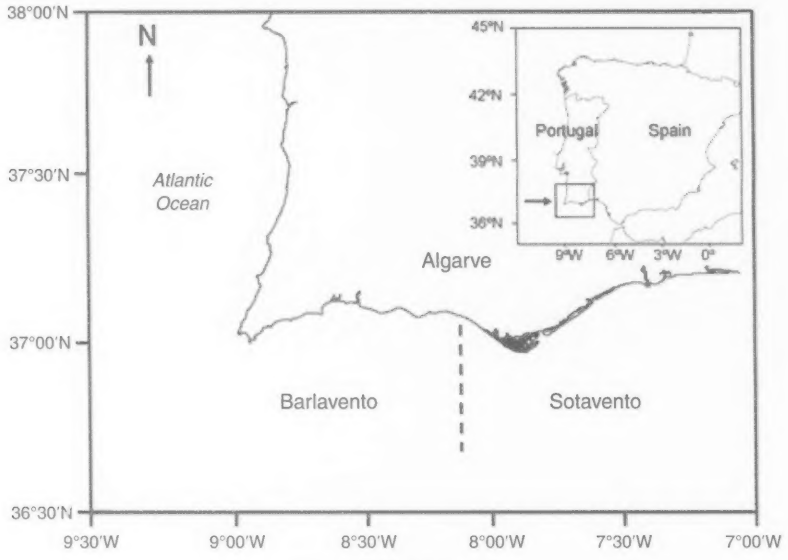

Figure 1

Map of the Algarve region and the Barlavento and Sotavento areas where the catches of deliberately lost traps of two types were quantified in 1999 and 2000, and where information on the numbers of traps lost by commercial fishermen and the reasons for trap loss were obtained by means of questionnaire surveys.

opening at the top (Fig. 3). Murejonas targeting sea breams (Sparidae) were baited with approximately 0.5 kg of crushed common cockle (*Cerastoderma edule*).

The octopus traps located in shallow waters were monitored by scuba divers using slates, video, and still photography cameras. Acoustic pingers, an acoustic receiver, and a GPS differential antenna were used to aid divers in locating the experimental traps. Data recorded consisted of the number of the trap, number and identification of the species captured, as well as an estimate of the total length of each individual caught. In order to estimate the total catch (numbers of fish), traps were also inspected for remains of fish that might have died or been eaten while inside the traps. The structural integrity of the traps was evaluated by divers one year after their deployment.

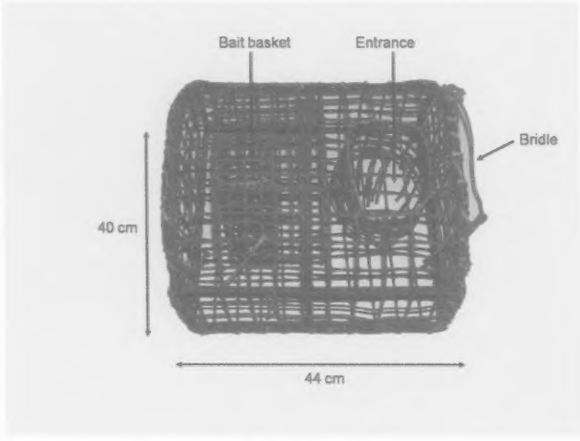

Figure 2

View from the top of an iron frame, plastic mesh octopus trap (covo) of typical dimensions (40×44×25 cm) and mesh size (4-cm plastic square mesh).

The catches were analyzed in terms of target vs. nontarget and prey (both target and nontarget) vs. predator species. The target species were common octopus (*Octopus vulgaris*) for the octopus traps, and Sparidae (axillary seabream (*Pagellus acarne*), common pandora (*P. erythrinus*), striped seabream (*Lithognathus mormyrus*), annular seabream (*Diplodus annularis*), Senegal seabream (*D. bellottii*), common seabream (D. *sargus*), two-banded seabream (*D. vulgaris*), black seabream (*Spondyliosoma cantharus*), and blotched picarel (*Spicara maena*) for the murejona fish traps. Conger eel (*Conger conger*), Mediterranean moray eel (*Muraena helena*), forkbeard (*Phycis phycis*), and *O. vulgaris* were considered predator species that would feed on trapped small fish and in the case of conger and moray eels, also on octopus.

For each trap type, the Zhou and Shirley (1997) model for the relationship between catch and soak time for baited traps where escapement is possible was fitted by nonlinear least squares regression to the catch-per-trap data with PROC NLIN software (SAS Institute Inc., Cary, NC.) and the equation:

$$C(t) = ab + a(t - b)e^{-ct},$$

where $C(t)$ = catch in numbers per trap haul;
t = soak time in days; and
a, b, and c are parameters to be estimated.

For this model, catch is zero at $t = 0$, the asymptotic catch after an infinite soak time is the product ab, and maximal catch C_{max} is attained at a soak time of $t_{max} = 1/c + b$:

$$C_{max} = ab + ac^{-1}e^{-(1+cb)}.$$

Quantification of trap loss

Questionnaires were used to survey fishing-boat skippers at ten ports of the Algarve, South of Portugal. The questionnaires were divided between the following areas (area—Barlavento, western Algarve and Sotavento, eastern Algarve) and by port and fishing vessel (local or coastal). The questionnaires were designed to quantify the number and type of traps used, the number lost per year, reasons for loss, and the degree of success in recovery attempts.

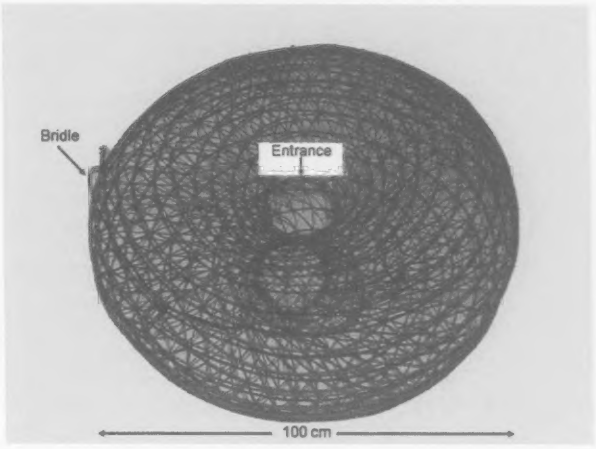

Figure 3

View from the top of a wire fish trap (murejona) showing the funnel-shaped entrance. The diameter is 100 cm, the height 35 cm, and the sides of the triangular wire meshes are approximately 2.5 cm.

Results

Catches in deliberately lost traps

Lost octopus traps caught six species: *O. vulgaris, C. conger, M. helena*, red scorpionfish (*Scorpaena notata*), comber (*Serranus cabrilla*), and *P. phycis*. Catch rates were generally low and highly variable (Fig. 4). Most octopus were captured in the first two weeks after trap deployment, and few catches were observed thereafter. For other fishes, namely small red scorpionfish, occasional catches were recorded up to three months after deployment. The estimated parameters of the Zhou and Shirley (1997) model were $a = 3.8576$, $b = 0.0318$, and $c = 2.292$. Based on these parameters the maximal catch is attained within 24 hours after deployment (0.47 days), and the asymptotic catch rate is 0.12 individuals per trap.

In addition to all six species caught by the octopus traps, fish traps caught damselfish (*Chromis chromis*), Mediterranean rainbow wrasse (*Coris julis*), *D. annularis, D. bellottii, D. vulgaris, S. cantharus,* Baillon's wrasse (*Symphodus bailloni*), and axillary wrasse (*S. mediterraneus*) and a maximum diversity of 10 species was attained 27 days after deployment. The most abundantly caught species was *D. vulgaris* that accounted for 43% of the fish observed in the traps, followed by *D. bellottii* (16%). Although most of the species were small, some larger fish, namely *C. conger,* were also found in the traps.

The mean number of individuals per trap peaked approximately two weeks after deployment and was followed by a sharp decrease from week 4 to 5, and then averaged approximately one fish per trap up to the end of the three month monitoring period (Fig. 5). The estimated maximal catch, based on the parameters of the Zhou and Shirley (1997) model (a=1.5397, b=0.5669, and c=0.1101) occurred 9.7 days after deployment, and the asymptotic catch rate was 0.87 individuals per trap. The same pattern of an initial increase in catches, followed by a decline, was seen in the catches of the most abundantly caught species (*D. vulgaris*) in individual fish traps (Fig. 6).

The fish trap predator-to-prey ratio, with predators considered to be *C. conger, O. vulgaris, M. helena,* and *P. phycis*, showed an opposite trend, increasing sharply from week 4 to 5 to a maximum of 2.0 35 days after deployment, then leveling off (Fig. 5). The initial high number of fish observed in the fish traps was largely due to the presence of the target species (Sparidae), whereas the predators, especially the three fish species *C. conger, M. helena, and P. phycis* were relatively more abundant 55, 71, and 89 days after deployment.

Whereas the iron frame octopus traps retained their structural integrity 12 months after deployment, the wire fish traps were completely destroyed.

Quantification of trap loss

A total of 84 interviews were conducted, representing 19.4% of the boats registered in the Algarve (southern

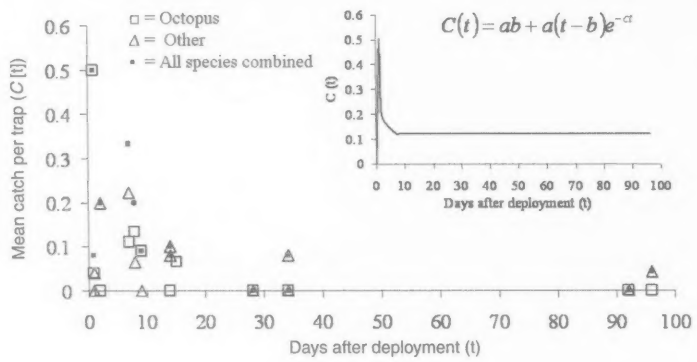
□ = Octopus
Δ = Other
▪ = All species combined
$C(t) = ab + a(t-b)e^{-ct}$
Mean catch per trap (C [t])
Days after deployment (t)
C (t)
Days after deployment (t)

Figure 4

Octopus trap catch rates (mean number per trap) over time. Inset figure is the fitted catch model of Zhou and Shirley (1997) with a = 3.8576, b = 0.0318, and c = 2.292.

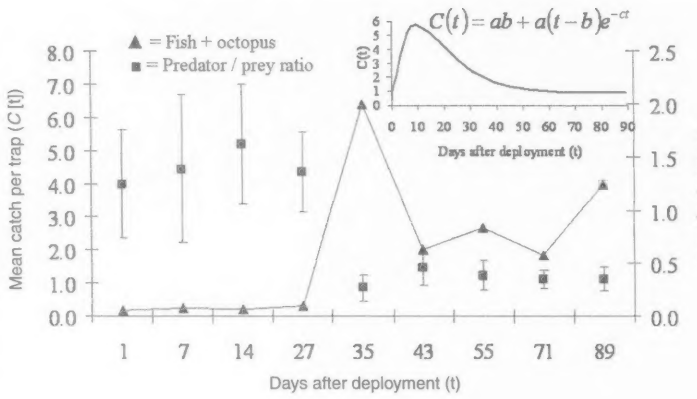
▲ = Fish + octopus
■ = Predator / prey ratio
$C(t) = ab + a(t-b)e^{-ct}$
Mean catch per trap (C [t])
Predator/prey ratio
Days after deployment (t)
C(t)
Days after deployment (t)

Figure 5

Murejona catch rates (C) (mean number per trap) over time. Mean ±SE (standard error) number of fish and octopus per trap, and the predator-to-prey ratio. Predators were conger eel (*Conger conger*), forkbeard (*Phycis phycis*), Mediterranean moray eel (*Muraena helena*), and common octopus (*Octopus vulgaris*), whereas prey were all other finfish species. Inset figure is the fitted catch model of Zhou and Shirley (1997) with a = 1.5397, b = 0.5669, and c = 0.1101.

region of Portugal) with licenses for fishing with traps. Of these, 13 boats had to be excluded from the survey because traps had not been used during the past year. Thus, questionnaire surveys were completed for 71 fishing boats that had been used to fish with traps. The results of the questionnaire survey are summarized in Tables 1 and 2.

All skippers surveyed that had fished with octopus traps had the particular type of small trap (covo) used to catch octopus. However, some of the boats also possessed other types of traps, generally of a larger size that were used to target other species. Thus, 16 (22.5 %) of the skippers interviewed had also used larger traps, mostly to catch cuttlefish, and two (2.8 %) of the skippers from the western area (Barlavento), had used murejona wire fish traps to capture fish, especially sea breams. These results confirmed the relative importance of covo-style traps as a gear.

Table 1

Summary of survey information collected from 84 interviews with skippers: mean depth fished, mean number of traps used by the different fleets (local and coastal) in the two areas (Barlavento and Sotavento), and mean numbers of traps lost per year per fishing vessel. SD = standard deviation.

		Mean number (±SD) of traps fished			Mean number (±SD) of traps lost		
Fleet region and area	Mean (±SD) depth (m) fished	Octopus trap	Cuttlefish trap	Fish trap	Octopus trap	Cuttlefish trap	Fish trap
Local (<9 m)							
Barlavento	19.1 ±5.7	270.3 ±200.5	149.0 ±145.2	190 ±7.1	30.9 ±55.5	78.8 ±147.5	13.5 ±10.6
Sotavento	21.1 ±5.0	644.4 ±261.7	112.5 ±75.0		145.6 ±102.2	13.5 ±11.1	
Coastal (>9m)							
Sotavento	25.0 ±5.0	903.8 ±227.7	80.0		318.5 ±207.8	10.0	

Table 2

Estimates of numbers of octopus traps lost per year off the coast of Barlavento and Sotavento of southern Portugal based on national statistics and questionnaire surveys. Fleet was separated into a local and coastal category. Number of licenses was the number of trap licenses issued (from national statistics). Number fishing was the number of boats fishing traps (from national statistics), Mean number of traps/boat was the mean number of traps fished per year (determined from questionnaires). Total number of traps in use was the product of the mean number of traps fished and the number of fishing vessels. Proportion of traps lost was estimated from the number of traps lost (from questionnaires) divided by the number of traps fished. Traps lost per year was the product of the proportion lost and the total number used.

Fleet	Area	Number of Licenses	Number of boats fishing	Mean number of traps/boat	Total number of traps used	Proportion of traps lost	Number of traps lost per year
Local (<9 m)	Barlavento	190	161	270.3	43,518	0.11	4975
	Sotavento	103	87	644.4	56,063	0.23	12,667
Coastal (>9 m)	Barlavento	58	49	995	48,755	0.21	10,437
	Sotavento	91	77	903.8	69,593	0.35	24,525
Total		442	374	2813.5	217,929	0.24	52,604

Although fish traps are relatively less important compared to the octopus traps, they are restricted to a particular use by the Algarve fishing fleet. The use of large fish traps in the Barlavento area is favored because of the hard bottom where there are larger concentrations of fish. The average numbers of traps used per boat for the three types of traps commonly used in the fishery, by port category (local or coastal) and coastal zone area, are given in Table 1. The octopus traps are by far the most common of all the traps used.

We estimated that 52,604 octopus traps were lost in Algarve waters in 2000, with the coastal fleet accounting for more losses than the local fleet, and higher losses in the Sotavento than in the Barlavento area (Table 2). Regarding the big traps used mostly to catch cuttlefish the local fleet lost more such traps than the coastal fleet, and there were more losses in the Sotavento than in the Barlavento area.

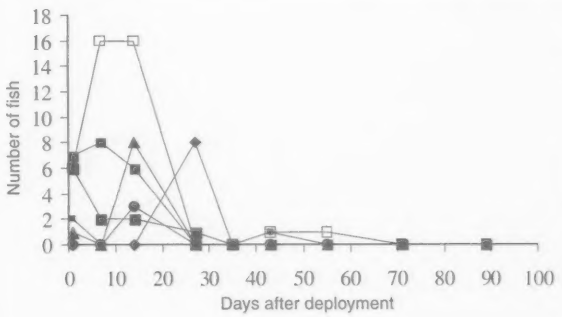

Figure 6

Number of two-banded sea bream (*Diplodus vulgaris*) observed in eight different traps over three months. Each symbol represents the catches of one trap.

The most important cause for the loss of traps was interaction with other gears (41%), followed by bad weather (39%), and fouling on rough bottom (18%). Skippers also indicated that gear loss could be caused by other factors (2%), especially theft. The main reason for trap loss in the local fishery was interference with other gears (42.6%) and fouling on rough bottom (42.4%) in the Sotavento and Barlavento areas. In the case of the coastal fishery, the main reasons for trap loss were bad weather (40.4 %) in the Sotavento area and interference with other gears in the Barlavento area (40.0 %).

Discussion

In comparison to the octopus traps, fish traps caught a greater variety of species and the average catch per trap (in the period of days to weeks after deployment) was much greater. Groups of individuals of the same species of Sparidae were recorded in the same trap, often on subsequent monitoring dates, indicating that escapement rates were low or that individuals that died or escaped were replaced by conspecifics (Bullimore et al., 2001). Abrasions on the head and snout from attempts to escape through the wire mesh also indicated that escapement rates were probably low (Bullimore et al., 2001; Al-Masroori et al., 2004). There was a succession in the capture of species; there were initially high catches of the target sea bream species, followed by the entry of larger predator-type species such as conger eel and fork beard. The predators were probably attracted by the smaller prey species within the trap, and the same individual predators were observed in the traps over weeks and in some cases for more than a month.

There have been relatively few studies on fish escapement rates from traps, and comparisons have generally not been possible because of differences in trap design and size. Munro (1974) reported that escapement from Antillean fish traps used in the Caribbean averaged 11.6% per day. Scarsbrook et al. (1988) reported a 0% escapement rate for sablefish (*Anoplopoma fimbria*). Al-Masroori et al. (2004) assumed a 10% escapement rate from large, single opening wire traps in Oman, and a 95% mortality rate for ghost-fishing traps. Given the design of the fish traps, our own observations of trapped fish, and the typical escapement rates reported in the literature, we believe that ghost fishing mortality rates of fish in the murejona traps are high and are caused by predation in the trap or are the result of injuries and starvation. On the other hand, we assume that octopus escapement rates were 100%. There may have been some trap-related mortality caused by predation because octopus require several minutes to exit a trap through the mesh and are therefore susceptible during that time to the attack of a moray eel or conger eel inside the trap.

Catches in octopus traps decline sharply 24 hours after deployment, whereas fish trap catches peak one to two weeks after deployment, and long after the bait has been consumed or has deteriorated. Rapid consumption of bait has been supported by the findings of Castro et al. (2005), who reported that fish discards in this region are completely scavenged within 24 hours, and by the general knowledge that octopus fishermen must rebait their traps frequently.

Optimal trap soak times of days or even weeks with asymptotic catch rates have been reported in a number of studies (Munro, 1974; Mahon and Hunte, 2001; Al-Masroori et al., 2004). Typically, as seen with our fish traps, catches tend to decline and stabilize at low rates for long soak times. Munro (1974) reported that for long soak times, catch rates in Antillian fish traps stabilized at the point where daily escapement equaled daily ingress.

Based on the relationship between rates of ingress, escapement, catch, and soak time, a variety of models have been used to model trap catches over time (Fogarty and Addison, 1997; Zhou and Shirley, 1997; Al-Masroori et al., 2004). The Zhou and Shirley (1997) is the only model where catches increase to a maximum of days or weeks after deployment and then decline, stabilizing at a low level. This model gave a good fit to the murejona data, where catches peaked two weeks after trap deployment, and then stabilized at a mean of approximately one fish per trap. Octopus trap catches also stabilized at very low catches per trap, but were highest 24 hours after deployment. A simple exponential model (Al-Masroori et al., 2004) adequately describes the catches over time but does not model the low residual catches. Thus, we opted to use the Zhou and Shirley (1997) model for the octopus trap data as well.

The results of the questionnaire survey showed that interaction with other gears (gear conflict) was the most important cause of trap loss. The large number of traps (often deployed without buoys at the surface to avoid theft) within a limited area where many other fishing vessels are operating simultaneously, coupled with long soak times, may explain these results. From our experience, fishermen who catch a longline of traps in their own gear often will simply cut the lines to disentangle the gears. Thus, the traps are often cut loose but fall close to where they had been fishing. The other major cause of trap loss was bad weather, often leading to the loss of entire longlines of traps. This cause is particularly important for the larger coastal vessels, which tend to fish further from their homeports and in deeper waters.

Given the fact that fishing with traps in the Algarve takes place in relatively shallow water, underwater surveys with divers are an appropriate method for monitoring catches in deliberately lost traps and for quantifying gear loss. Despite the problem of the loss of traps due to bad weather and interaction with commercial gear, it is possible to monitor both octopus and fish traps for prolonged periods. The use of divers permits the monitoring of traps and their catches without disturbance. This method is vital for understanding trap catch dynamics and the changes in catches after the bait used to attract fish and cephalopods is no longer present in

the traps. However, in order to be able to fully evaluate the effects of ghost fishing from the large number of traps that are lost each year in the coastal waters of southern Portugal, it will be necessary to investigate escapement rates, and to estimate mortality rates. Such investigations can be done by tagging trapped fish and monitoring their escapement and survival by divers.

Bycatch and ghost fishing mitigation measures for traps generally involve the use of escape mechanisms and the use of degradable materials (e.g., Scarsbrook et al., 1988). In the case of the fish traps, mitigation options are limited because the entire trap is made from wire and the trap door is on the bottom of the trap. Octopus traps have a hatch that can be attached with degradable material and the plastic netting could be replaced with biodegradable netting. However, perhaps the most important measure to reduce mortality would be the implementation of a code of conduct leading to less gear loss from gear interaction and theft.

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Age- and length-at-maturity of female arrowtooth flounder (*Atheresthes stomias*) in the Gulf of Alaska

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Arrowtooth flounder (*Atheresthes stomias*) has had the highest abundance of any groundfish species in the Gulf of Alaska since the 1970s (Matarese et al., 2003; Turnock et al., 2005; Blood et al., 2007); however, commercial catches have been restricted because Pacific halibut (*Hippoglossus stenolepis*) are caught as bycatch in the fishery. Arrowtooth flounder plays a key role in the ecosystem because it is a dominant organism within the food web, both as an apex predator of fish and invertebrates, as well as an important prey for walleye pollock (*Theragra chalcogramma*; Aydin et al., 2002). Walleye pollock is the dominant groundfish in the Bering Sea, a principal groundfish in the Gulf of Alaska, and the primary prey for marine mammals. The distribution of arrowtooth flounder extends from Cape Navarin and the eastern Sea of Okhotsk in Russia, across the Bering Sea, Aleutian Islands, Gulf of Alaska, and south to the coast of central California (Shuntov, 1964; Britt and Martin, 2001; Chetvergov, 2001; Weinberg et al., 2002; Zenger, 2004). Because of the importance of arrowtooth flounder in the marine ecosystem of Alaska, a maturity study of this species was undertaken to determine age-at-maturity, which is essential for age-based stock management models. Before these results, management has had to rely upon a length-at-maturity-based estimate (Zimmermann, 1997) to manage stocks in the Gulf of Alaska (GOA), Bering Sea, and Aleutian Islands. The central GOA was selected as the location for this maturity study because it contains approximately 70% of the total Gulf of Alaska arrowtooth flounder biomass (1.9×10^6 t, age 3 and older)— the highest percentage in the world (Shuntov, 1964; Britt and Martin, 2001; Weinberg et al., 2002; Wilderbuer and Nichol, 2006).

Materials and methods

All female arrowtooth flounder used in this study were collected with bottom trawls. The central GOA was initially sampled during February 2002 (Fig. 1) from the National Oceanic and Atmospheric Administration (NOAA) ship *Miller Freeman* during an Alaska Fisheries Science Center (AFSC) Recruitment Processes Program cruise (Blood et al., 2007). The area selected for trawling was sampled the prior year by the AFSC and had produced a high abundance of arrowtooth flounder eggs and larvae.

A second collection was made in July 2003 during the AFSC biennial GOA groundfish assessment survey. In both years, whole ovaries and otoliths were collected. All specimens were selected by using length-stratified sampling method so that three to seven females were collected for each cm interval of total body length larger than 18 cm.. The sampling protocol, histological methods, ovary maturity classifications, and aging methods followed those described in Stark (2007). Mature females were those specimens classified with ovary stages ranging from cortical alveoli to postovulatory follicles, which were the same criteria used by Zimmermann (1997) for a September 1993 GOA arrowtooth flounder maturity assessment. To investigate the consistency of oocyte maturation within the ovary, two additional sections were taken from the anterior and medial regions of both ovaries from 10 specimens collected during February 2002 and 10 specimens from July 2003. These sections were compared with the standard sample section taken from the posterior area of one ovary. For all the following procedures, S-Plus software was used (vers. 2000 Professional release 3, MathSoft Inc., Cambridge, MA). Maturity was estimated as a function of length and age by fitting a logistic function to the maturity data with generalized linear modeling (Venables, 1997). The significance of temporal differences was tested by fitting the model of maturity as a function of total body length (L) and age (A), including the date of sampling, and by recalculating without the date term. Significance of the date term was determined by using analysis of deviance (Venables, 1997). The variance of age (A_{50}) and total body length (L_{50}) at 50% maturity were estimated for February 2002 and July 2003 by using bootstrapping (Efron and Tibshirani, 1993) based on 200 resamplings with replacement of the maturity, age, and length data. February 2002 and July 2003 differences in the A_{50} and L_{50}were tested with a Z-test (Sokal, 1969). The February 2002 L_{50} result was also tested against the September 1993-based estimate by Zimmermann (1997) with a Z-test. To assess the temporal progression of ovary maturity between February 2002 and July 2003, ovary maturity classifications were summarized for females that had reached A_{50} as determined by this study.

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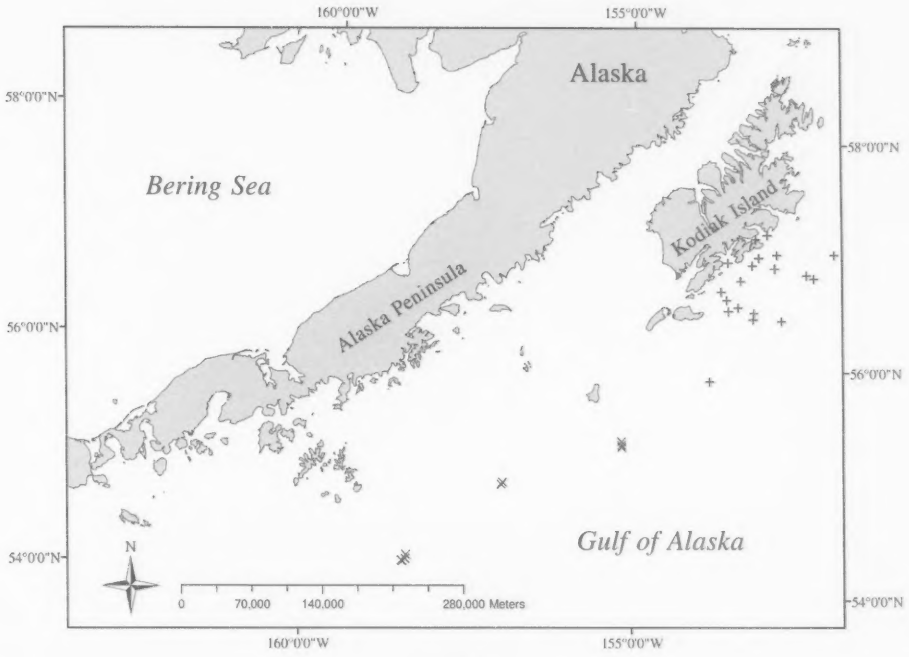

Figure 1

Locations where arrowtooth flounder (*Atheresthes stomias*) were collected by bottom trawl during National Oceanic and Atmospheric Administration Alaska Fisheries Science Center cruises during February 2002 (×) and July 2003 (+) in the Gulf of Alaska.

To determine if ovary growth occurred between February and July, the gonadosomatic index (somatic body weight/ovary weight, *I*G) of females $\geq A_{50}$ was determined by methods described by Stark (2007). The comparison did not include females with hydrated oocytes or postovulatory follicles.

Results

In the February 2002 collection, approximately 50% of the females were classified as spawning and 10% were nearing spawning condition (advanced yolk). By July, spawning activity was <5% but continuing, and 20% of the females were at the advanced yolk stage of maturity based on the 2003 collection.

Mature female arrowtooth flounder were found in every location where sample collections were made, namely on the outer continental shelf at 101–200 m depths and upper slope at 301–700 m depths, during February 2002. During July 2003, the locations and depths sampled ranged from the intertidal zone at 1–100 m down to the continental banks, gullies, and outer shelf at 101–200 m. Mature female specimens were as young as 3 years of age and 260 mm *L*.

This study was the first to determine that age was a significant predictor ($P<0.001$) of maturity for female arrowtooth flounder. The estimated age at 50% maturity (A_{50}) was 7.0 years, based on the February 2002 collection (Fig. 2, Table 1). The February 2002 result did not differ significantly ($P=0.38$) from the July 2003 result (6.6 years). Of the two results, the February 2002 A_{50} estimate had a much lower variance (Table 2) and consequently was the most reliable. The estimated length at which 50% of the females were mature (L_{50}) was 460 mm for the February 2002 collection (Fig. 3, Table 2) and did not differ ($P= 0.68$) for the July 2003 collection (464 mm). However, the variance of the L_{50} estimate was much lower for the February 2002 collection, and thus February represented the more optimal month for assessing arrowtooth flounder maturity. Oocyte development was consistent within the ovaries and between each ovary pair for every compared specimen. No significant growth occurred between February and July, based on the *I*G results, which declined from a mean of 3.6 *I*G in February 2002 ($n=167$) to 1.8 *I*G in July 2003 ($n=115$).

Discussion

This study was the first to establish arrowtooth flounder age-at-maturity. The estimated age at 50% maturity (A_{50}=7 years) in the GOA was based on the February

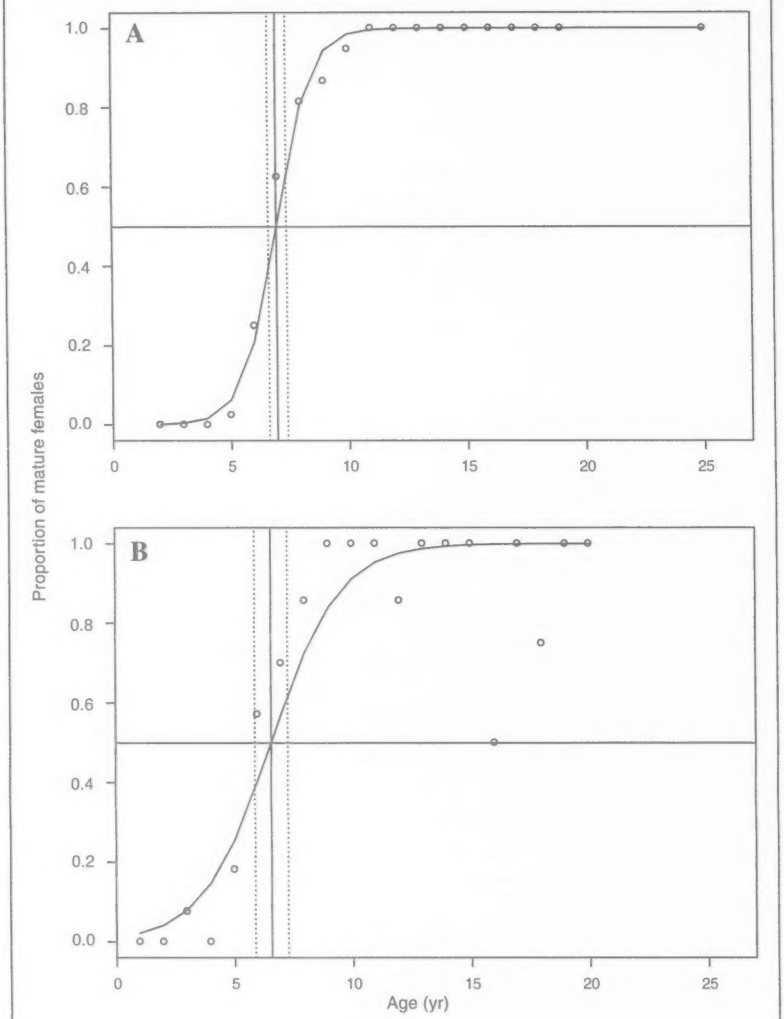

Figure 2

Maturity estimated as a function of age for female arrowtooth flounder (*Atheresthes stomias*) in the Gulf of Alaska by fitting a logistic function to the maturity data based on (**A**) the February 2002 (n=301) collection, and (**B**) the July 2003 (n=226) collection. Mean age at 50% maturity, indicated by the solid vertical lines, was 7.0 years (A) and 6.6 years (B) and 95% confidence intervals are represented by dotted lines.

2002 maturity collection results that were supported by the July 2003 results. Age-based estimates of maturity should be less variable, and less affected by changes in environmental conditions, population abundance, and spawning biomass levels than length-based estimates. Those changes can affect arrowtooth flounder growth rates. Growth was significantly faster for Pacific cod (*Gadus macrocephalus*) in the Bering Sea than in the Gulf of Alaska (Stark, 2007). Together with growth, cod L_{50} differed significantly (P<0.001) between areas; in contrast, cod A_{50} differed only slightly (P=0.02). Therefore, age-based maturity estimates should generally be considered the more reliable.

Although not as reliable, the estimated length-at-maturity of female arrowtooth flounder has remained stable in the GOA, based on the results of this study

Table 1

Female arrowtooth flounder (*Atheresthes stomias*) age-at-maturity results based on ovary histological samples (n) collected between the spawning and late spawning periods in the Gulf of Alaska by date of collection. The parameters of the logistic equation that were used to fit the data were the following: B (slope of the line) and A (y intercept), variance (the square of the standard deviation of B and A), covariance (the product of the standard deviations of B and A and the coefficient of correlation between them), age (years) at which 50% of females were expected to reach sexual maturity (A_{50}), and variance of A_{50}.

	Date of collection	
	February 2002	July 2003
n	301	226
B	1.3817	0.6835
A	−9.6183	−4.4945
Variance (B)	0.0077	0.0016
Variance (A)	1.7381	1.3528
Covariance (B, A)	0.0070	0.0007
A_{50}	6.9614	6.5754
Variance (A_{50})	0.0326	0.1448

Table 2

Female arrowtooth flounder (*Atheresthes stomias*) length-at-maturity results based on ovary histology samples (n) collected between the spawning and late spawning periods in the Gulf of Alaska by date of collection. The parameters of the logistic equation that were used to fit the data were the following: B (slope of the line) and A (y intercept), variance (the square of the standard deviation of B and A), covariance (the product of the standard deviations of B and A and the coefficient of correlation between them), length (mm) at which 50% of females were expected to reach sexual maturity (L_{50}), and variance of L_{50}.

	Date of collection	
	February 2002	July 2003
n	303	251
B	0.0455	0.0215
A	−20.9220	−9.9786
Variance (B)	1.1171	2.9534
Variance (A)	6.9072	6.3385
Covariance (B, A)	0.0002	−0.0002
$L_{50\,(mm)}$	459.6917	464.1629
Variance (L_{50})	27.5705	75.9320

and the 1993 maturity study results by Zimmermann (1997). For this present study, the estimated female L_{50} was 460 mm, which did not differ significantly (P=0.08) from the September 1993 L_{50} estimate of 469 mm. Currently, that length-at-maturity estimate is used to manage the arrowtooth flounder stocks of both the GOA and Bering Sea, because the A_{50} has not been known. Consequently, with the use of the age-at-maturity estimates determined in the present study, the estimates of arrowtooth flounder abundance would be expected to improve significantly within the stock management model.

Stock management would also benefit from a determination of the arrowtooth flounder annual spawning period. The arrowtooth flounder spawning period probably begins in December, based on results from the AFSC ichthyoplankton surveys in the Gulf of Alaska, during which developing embryos and larvae were found at the end of January (Blood et al., 2007). The rate of spawning declined from February 2002 (50%) to July 2003 (<5%), according to this study. Spawning may conclude at the end of summer because Zimmermann (1997) found no spawning females during September. Therefore, the overall spawning period of arrowtooth flounder appears to extend for over 8 months or more in the GOA. This is a longer spawning period than has been found for other principal groundfish species in Alaska, which have spawning periods of 6 months or less (Matarese et al., 2003; Stark, 2004, 2007). A protracted spawning period could promote stock recruitment by increasing the dispersion of progeny and thereby increasing the probability of placing progeny in a favorable rearing environment. Turnock et al. (2005) estimated that the spawning biomass of female arrowtooth flounder has increased annually since 1961 (1.98×10^5 t) and remains above 1.24×10^6 t in the GOA. Similarly, the spawning biomass was estimated to be at its highest level ever recorded in the Bering Sea and Aleutian Islands, at more than 8.24×10^5 t (Wilderbuer and Nichol, 2006). However, the size of the spawning biomass may be overestimated for the Bering Sea and Aleutian Islands because of the reliance on the Gulf of Alaska L_{50} estimate for the Bering Sea and Aleutian Islands management model. This overestimate could occur if the rate of female arrowtooth flounder growth was significantly higher for the Bering Sea and Aleutian Islands population than it was for the Gulf of Alaska population. A significantly higher rate of growth could result in a significantly larger L_{50}, which could lower the spawning biomass estimate by excluding smaller females that may have been mature. Therefore, the estimates of the arrowtooth flounder spawning biomass that are determined by stock managers should be more reliable after the current length-based maturity models are replaced with age-based maturity models using the A_{50} estimate from this study.

Conclusions

Arrowtooth flounder has consistently been the most abundant groundfish species in the Gulf of Alaska because of its high levels of recruitment and low fishing-induced mortality. Age was found to be a significant

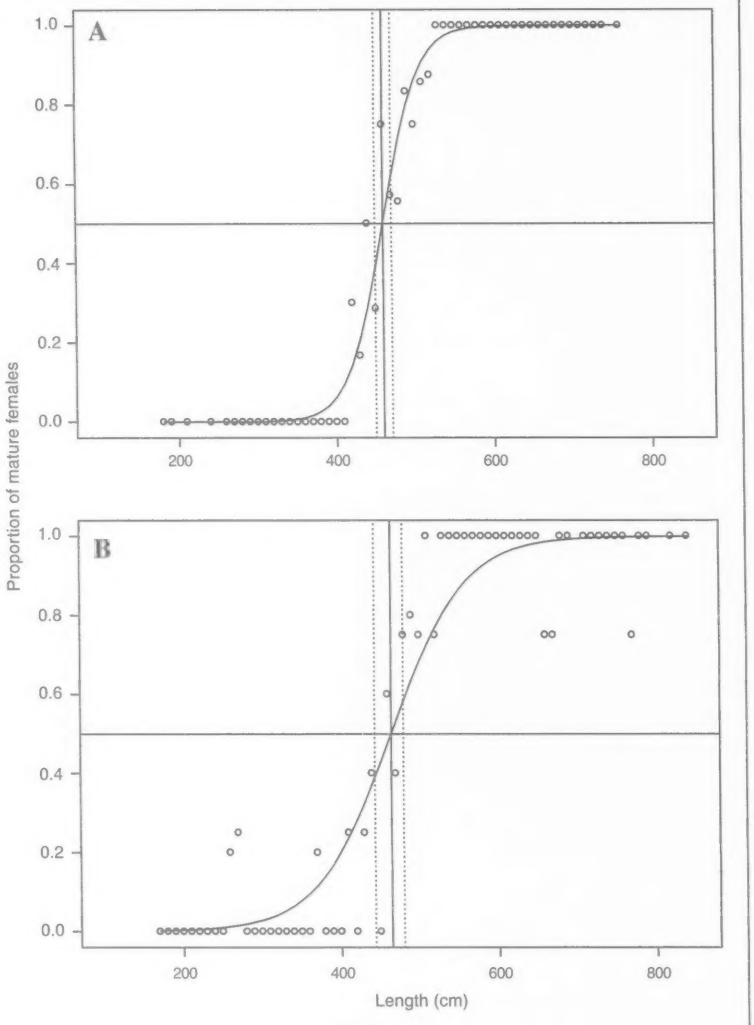

Figure 3

Maturity estimated as a function of total length (L) for female arrowtooth flounder (*Atheresthes stomias*) in the Gulf of Alaska by fitting a logistic function to the maturity data based on the (**A**) February 2002 collection (n=303), and (**B**) July 2003 collection (n=251). Mean length at 50% maturity, indicated by solid vertical lines, was 460 mm (A) and 464 mm (B) and 95% confidence intervals are represented by dotted lines.

predictor of female maturity in this study and a mean age-at-maturity (A_{50}, 7 years) was established for female arrowtooth flounder that will allow for the development of an improved stock management model. The model should provide more reliable estimates of arrowtooth flounder abundance in the Gulf of Alaska as well as the Bering Sea. This study also documented the total body length (L 460 mm) at which 50% of the females are mature in the Gulf of Alaska—an estimate that did not differ significantly from a 1993-based estimate.

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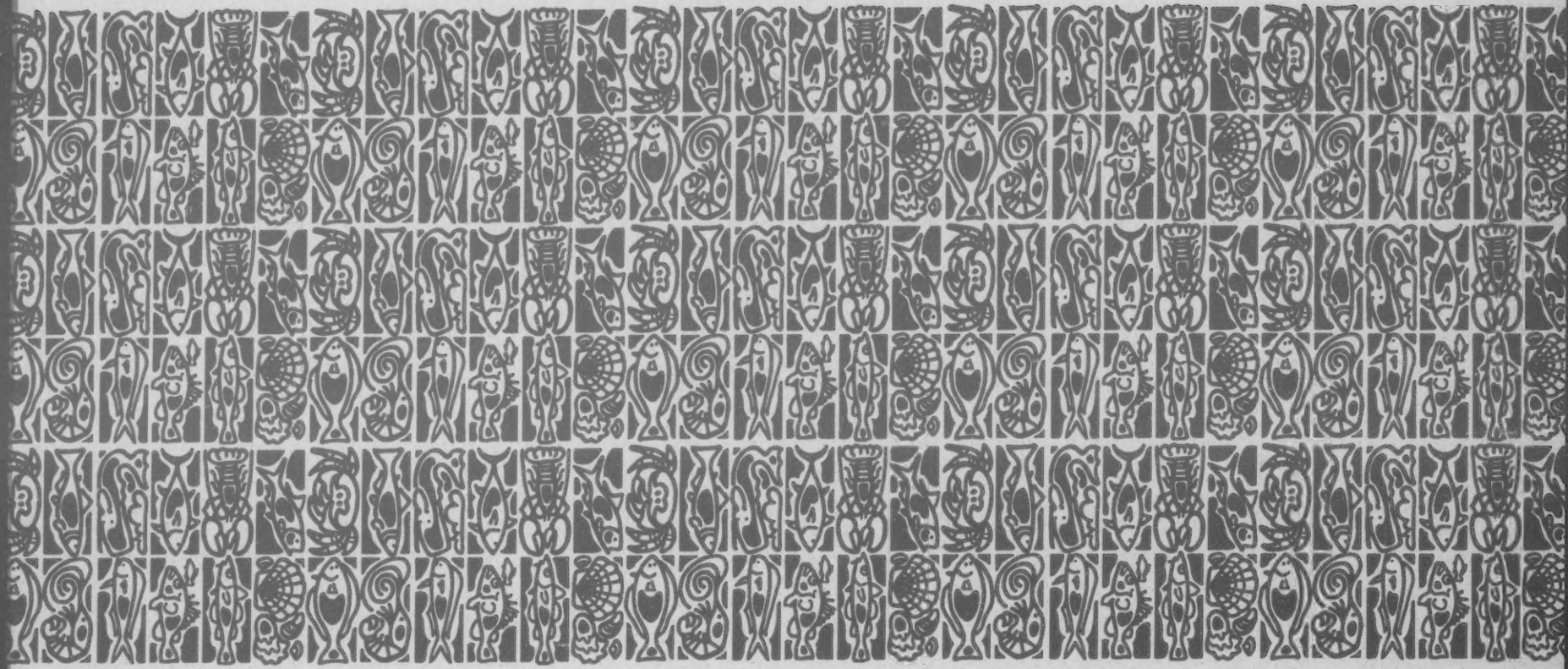
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